Deer in Britain: population spread and the implications for biodiversity

PALMER, GEORGINA

Deer in Britain: population spread and the implications for biodiversity

Georgina Palmer

School of Biological and Biomedical Sciences,

Durham University

2014

This thesis is submitted in candidature for the degree of

Doctor of Philosophy

Declaration

The material contained within this thesis has not previously been submitted for a degree at Durham University or any other University. The research reported within this thesis has been conducted by the author unless indicated otherwise.

Abstract

Owing to their cascading effects on ecosystems, keystone species should be a focus of conservation and management efforts. However, in order to manage populations of keystone species – such as deer – effectively, there is a need to quantify how the distribution and abundance of populations may change in the future, and to understand the potential consequences of these changes for biodiversity.

By relating species' abundance data within their historic ranges to habitat variables, I developed a novel methodology to assess habitat suitability for deer across Britain, none of which are currently at equilibrium with their environment. The resultant models performed well in describing the observed, contemporary distribution of roe *Capreolus capreolus*, red *Cervus elaphus* and Chinese muntjac deer *Muntiacus reevesi* in Britain. In particular, the model for the non-native muntjac deer highlighted the potential for this species to expand its range significantly in the future.

I estimated, for the first time, the rate and pattern of the future spread of deer at a landscape scale across Britain, using a spatially explicit population model (SEPM). The SEPM accounts for range-limiting processes such as species-specific dispersal ability and environmental barriers to dispersal. The SEPM performed well in describing the observed spread of roe, red and muntjac deer in Britain between 1972 and 2007, and predicted the spread of, and overlap between, species to continue to increase in the future. From sensitivity analyses, I found that the spread of deer was strongly influenced by adult and juvenile survival.

I also investigated the impacts of deer on their environment using two approaches. First, using vegetation data collected in 35 woodland sites across Britain, I found negative relationships between the density of roe deer and the diversity and abundance of shrub-layer vegetation. Second, I investigated the potential cascading effect of this negative relationship between deer density and shrub layer vegetation on bird populations. I used a long-running dataset on bird abundances across Britain, to construct and contrast two multi-species composite population trends for birds: one for deer-sensitive woodland birds and the second for deer-tolerant woodland birds. The divergence in these trends showed a striking association to a composite population trend for deer (also calculated using data from long-running volunteer

surveys). These results demonstrate the potential for rapid and profound impacts of keystone herbivores across multiple tropic levels, which are likely to increase as a consequence of the predicted future expansion of such species.

Acknowledgements

Firstly, I would like to say a huge thank you to my supervisors, Steve Willis, Phil Stephens and Alastair Ward, for their help, support and encouragement during my time in Durham. I would also like to thank Shane Richards for many helpful discussions, and David Roy and Stuart Newson for their collaboration on this project.

Data were kindly provided from a number of sources: the British Deer Society, the Centre for Ecology and Hydrology, the British Trust for Ornithology, the Ministry of Defence (particular thanks to Rosie Rowe and Paul Johnson), and the Hertfordshire Natural History Society.

This work was generously funded by the Whitehead Trust, and additional financial support was provided by St. Mary's College, Durham University.

Thanks go to Ian Smales and Kate Risley for their time, Marco Apollonio for his hospitality, and to Robin Gill and Brenda Mayle for providing copies of out-of-print articles and reports. I would also like to thank all of the members of the lab for their tea, biscuits and endless encouragement. Naiara and Andy, I can't thank you enough. Special thanks must go to Steve Hancock for his help with analysing photographs and coding, and to Robi Bagchi and Tom Mason for their patience and help whilst I learnt the inner workings of *R*. Thanks must also go to my Dad, who was my trusty fieldwork assistant during the summer of 2011.

Finally, a massive thank you to my family and friends who shared the ups and downs of the past few years. I couldn't have done it without you.

This thesis is dedicated to my parents, Andria and John.

Thank you for everything.

Table of contents

List of tables

List of figures

List of abbreviations

AIC	Akaike's information criterion
AUC	Area under a receiver operating characteristic curve
BBS	Breeding bird survey
BDS	British Deer Society
BMS	Butterfly monitoring scheme
BTO	British Trust for Ornithology
CCW	Countryside Council for Wales
CEH	Centre for Ecology and Hydrology
CNCC	Council for Nature Conservation and Countryside
CWD	Chinese water deer
DVC	Deer-vehicle collision
ENFA	Ecological niche factor analysis
GWCT	Game and Wildlife Conservation Trust
GDD5	Growing degree days above 5°C
JNCC	Joint Nature Conservation Committee
LCM2000	Land cover map 2000
MTCO	Mean temperature of the coldest month
NBN	National Biodiversity Network
NGC	National Gamebag Census
SDM	Species distribution model
SEPM	Spatially explicit population model
SNH	Scottish Natural Heritage

Chapter 1 : General introduction

1.1. Motivation

Herbivorous ungulates play a key role in shaping communities from temperate to tropical systems (Cumming et al. 1997, Rooney and Waller 2003, Côté et al. 2004). In recent decades, populations of many such species have increased dramatically (Côté et al. 2004, Hemami et al. 2005, Apollonio et al. 2008), and have been shown to exert cascading effects on other components of biodiversity in ecosystems they inhabit (Fuller and Gill 2001, Côté et al. 2004, Ripple and Beschta 2012, White 2012). These effects are commonly mediated through changes to vegetation abundance, structure, diversity and composition (Zalba and Cozzani 2004) which, in turn, has impacts on taxa including – but not exclusively – birds (Zalba and Cozzani 2004, Allombert et al. 2005a), small mammals (Côté et al. 2004), and invertebrates (Pollard and Cooke 1994, Allombert et al. 2005b). Owing to their cascading effects on ecosystems, keystone species should be a focus of conservation and management efforts (Simberloff 1998) so that stable and diverse ecosystems are maintained. However, identifying, quantifying, understanding and predicting the mechanisms of their impacts across communities is problematic given the difficulties in monitoring whole ecosystems. As a first step towards managing ungulate populations effectively, there is a need to quantify how their distribution and abundance may change in the future, and then to understand the potential consequences of these changes for biodiversity (Cumming et al. 1997, Rooney and Waller 2003, Côté et al. 2004, Ward 2005).

In this thesis I focus on deer, which are a valuable component of ecosystems, both economically and ecologically (Apollonio et al. 2008, P.O.S.T. 2009, Perez-Espona et al. 2009). They provide income through venison production and sport hunting, and at moderate densities they can have positive impacts within the ecosystems they inhabit, because grazing provides a more diverse vegetation structure and species composition (Putman 1988, Mitchell and Kirby 1990). Deer are the most widespread and abundant large mammals in the world, with approximately 40 species indigenous to all continents with the exception of Antarctica and Australia (Chaplin 1977). However, most scientific research has focussed on deer in temperate regions – particularly white-tailed deer *Odocoileus virginianus* in America, and on red deer *Cervus elaphus* and roe deer *Capreolus capreolus* in Europe. The range and abundance of deer in temperate regions have increased rapidly in the last few decades (McShea et al. 1997,

Côté et al. 2004, Ward 2005). As a result of this, there is growing concern regarding the cascading impacts these keystone species have in the environments they occupy (McShea and Rappole 1992, Waller and Alverson 1997, Fuller and Gill 2001, Hemami et al. 2005, Greenwald et al. 2008, White 2012). Given these concerns, and the ecological and economic interest in deer, it is surprising that predictions of future changes in their abundance, distribution and impact are rare in the literature (but see Chapman et al. 1994, Ward 2005, Acevedo et al. 2011, Gormley et al. 2011, Tanentzap et al. 2013). Such information is crucial in determining locations where pre-emptive management may be necessary – and best placed – to regulate and conserve deer populations as well as other components of biodiversity. To address this deficit, I aim to create a dynamic distribution model which can be used to predict the potential future distributions of deer, and to investigate factors affecting their spread. I will also investigate how changes in deer abundance influence taxa other than deer.

1.2. Outline of the introduction

The remainder of this introduction is split into four sections. First, I describe methodology to predict the potential future distribution of species. Second, I discuss the current status of research on the impacts of deer on their environment, with particular emphasis on the current state of research on British deer. Third, I describe the ecology and distribution of my study species. Finally, I describe the structure and aims of this thesis.

1.3. Modelling species distributions

In recent decades, the abundance and distribution of herbivorous ungulates in temperate regions have increased rapidly (McShea et al. 1997, Côté et al. 2004, Ward 2005). One of the reasons for these increases is the increase in afforestation, a favoured habitat for many species (Putman and Moore 1998, Fuller and Gill 2001, Ward 2005, P.O.S.T. 2009). Other factors which have influenced the increase in ungulate populations include:

- deliberate releases and escapes from enclosed populations (Chapman et al. 1994, Fuller and Gill 2001, Ward 2005, Dolman and Waber 2008, British Deer Society 2010c);

- changes to game management practices and legislation (Fuller and Gill 2001, Côté et al. 2004, Allombert et al. 2005b);
- changes to agricultural routines such as increases in winter crop availability, as well as an increase in agricultural set-aside (Putman and Moore 1998, Côté et al. 2004, P.O.S.T. 2009);
- a reduction in livestock husbandry, therefore increasing resources for deer (Fuller and Gill 2001);
- a reduction in hunting (McShea et al. 1997, Fuller and Gill 2001, Côté et al. 2004);
- loss of natural predators (Breitenmoser 1998 in Fuller and Gill 2001, Côté et al. 2004, Allombert et al. 2005a);
- changes in climate (Fuller and Gill 2001, P.O.S.T. 2009) – warmer winter and spring weather has been correlated with increased birth weight and survival of deer (e.g. Albon et al. 1983); and
- changes in woodland management, such as thinning and coppicing (Gill 2000).

Despite many studies stating that observed increases in the distribution and abundance of deer will continue in the future (Fuller and Gill 2001, Ward 2005, Ward et al. 2008), predictions of the scale and rate of these increases have rarely been produced (but see Chapman et al. 1994, Acevedo et al. 2011). Both of the latter studies used correlative species distribution models (SDMs), which relate the occurrence of a species to environmental variables. Although this approach is the most commonly used method to predict the future distributions of species (e.g. invertebrates: Hill et al. 2002, amphibians and reptiles: Araujo et al. 2006, mammals: Thuiller et al. 2006a, Levinsky et al. 2007, plants: Franklin et al. 2013), mechanistic models are widely acknowledged as the 'next-step' in producing more realistic predictions of spread (Keith et al. 2008, Kearney and Porter 2009, Willis et al. 2009, Huntley et al. 2010, Merow et al. 2011, Fordham et al. 2012, Fennell et al. 2013).

At their simplest, correlative SDMs attempt to describe the relationship between species occurrence (or absence) and environmental conditions. This relationship is then projected (or retrodicted) in time and/or space to simulate the occurrence of environmentally suitable areas (Kearney and Porter 2009). Biophysical, mechanistic

models utilise data on species' tolerances to environmental conditions (obtained from laboratory-based experiments) to refine predictions obtained from correlative models (e.g. Kearney et al. 2008, Kearney and Porter 2009, Elith et al. 2010). For example, Kearney *et al.* (2008) determined the temperature limits to movement, survival and reproduction of the cane toad *Bufo marinus* in Australia. They then identified locations where temperatures would not exceed or fall below these critical temperature thresholds, to define areas where this species may be able to colonise under future climate change. The authors found that much of southern Australia – which was originally predicted to be suitable using correlative SDMs (e.g. van Beurden 1981, Urban et al. 2007) – would fall outside of favourable conditions for movement; in turn, this would limit the toads' ability to breed, forage and therefore survive (Kearney et al. 2008). However, environmental conditions are not the sole determinants of where a species can be found. Others factors include inter- and intra-specific competition, physiological tolerances, disease, barriers to dispersal, anthropogenic factors, and species-specific dispersal abilities. Spatially explicit population models (SEPMs) incorporate some or all of these processes, and therefore provide a better reflection of potential ranges than correlative approaches. Although SEPMs require more data than correlative approaches, this often results in increased biological realism.

Spatially explicit, mechanistic species distribution models

SEPMs couple together a (potentially individual-based) population model with a spatially explicit map of heterogeneous environmental suitability (Dunning et al. 1995). SEPMs can be used to predict species distributions, to determine key demographic parameters which limit distributions, and to determine the impact of adaptive (species or habitat) management strategies to control or enhance a species' spread (Dunning et al. 1995). For example, Rushton *et al.* (1997) used a SPEM to model the distribution of native red squirrels *Sciurus vulgaris* and non-native grey squirrels *S. carolinensis* in Britain. First, the authors' defined habitat across the U.K. as being either suitable or unsuitable based on the known preferences and requirements of each species. Then, population size in each location of suitable habitat was determined on a yearly basis using species-specific reproduction, survival and dispersal rates (Figure 1-1). Dispersal occurred in response to intra-specific competition, and red squirrel breeding success was reduced wherever the two species co-occurred, in response to interference

competition. The authors used their model to predict the spread of squirrels in Norfolk, with and without accounting for inter-specific competition. They simulated red squirrel persistence where grey squirrels did not invade their habitats. However, when grey squirrels were predicted to colonise an area containing red squirrels, the survival (and consequently the distribution) of red squirrels would decrease. This result matched observations of decreases in red squirrel populations in Norfolk, and was taken to indicate that interference competition was likely to be a primary mechanism causing the observed decline of red squirrel abundances.

The major criticism of SEPMs is the large amount of demographic data they require; these data are often difficult to obtain for the species of interest, especially if they are poorly studied (Ruckelshaus et al. 1997, Naujokaitis-Lewis et al. 2009). Despite this, SEPMs have produced robust predictions of the distributions of a wide variety of species (e.g. Pulliam et al. 1992, Collingham et al. 1996, Rushton et al. 1996, Rushton et al. 1997, Willis et al. 2009, Marucco and McIntire 2010), and have highlighted the potential for such approaches to be used as powerful tools in the management of species (Dunning et al. 1995, Rushton et al. 1997). Given the economic, cultural and ecological importance of ungulates across the globe, and the large body of research focused on them, it is surprising that spatially-explicit, mechanistic predictions of how their distributions may change in the future are currently rare in the literature (but see e.g. Holdo et al. 2011, Lopez-Alfaro et al. 2012).

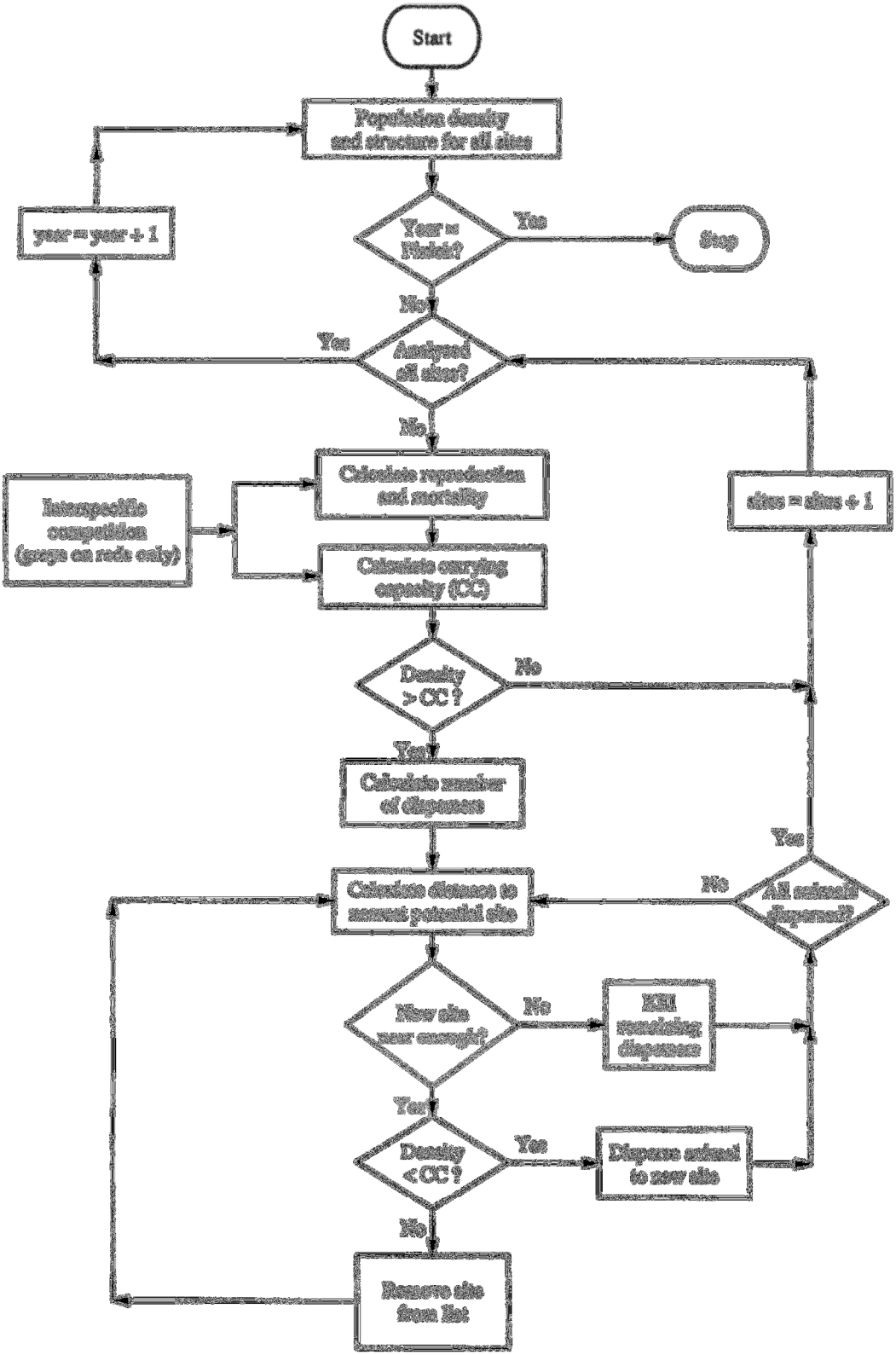


Figure 1-1. Flow chart showing the population model used by Rushton *et al.* (1997) to predict the distribution of red *Sciurus vulgaris* and grey squirrels *S. carolinensis* in Britain. Image taken from Rushton *et al.* (1997).

1.4. Impacts of deer

Deer often act as keystone species in many of the habitats they occupy (McShea and Rappole 1992, Waller and Alverson 1997, Fuller and Gill 2001, Dolman and Waber 2008, Greenwald et al. 2008, White 2012). Many studies have shown that the abundance and diversity of a wide range of taxa have been modified by direct and indirect effects of increasing deer pressure upon the areas they inhabit (see Côté et al. 2004 for a review). These studies usually assess the impacts of deer on single components of ecosystems and usually at single sites. To my knowledge, there have been very few field studies assessing the impacts of individual deer species, or combinations of species, on communities within different trophic levels (see e.g. Bressette et al. 2012), despite reviews that have raised awareness of cascading effects (Gill 2000, Fuller and Gill 2001).

As herbivorous ungulates, the primary mechanism by which deer alter their environment is through their impact on vegetation (Putman and Moore 1998). Although some studies have assessed impacts within habitats such as salt marshes (Diaz et al. 2005, Hannaford et al. 2006), heathland (Hester et al. 1999) and agricultural land (Putman and Moore 1998), the majority of studies assessing the impacts of deer have been carried out within woodland habitats (e.g. Kay 1993, Gill and Beardall 2001, Sage et al. 2004, Rossell et al. 2005, Bressette et al. 2012). The impacts of increased grazing pressure on woodland biodiversity are summarised by Mitchell and Kirby (1990) (Table 1-1). In temperate woodlands, excessively grazed areas generally have no shrub layer, trees are barked and stripped and in the ground layer there are extensive bare patches interspersed with weed species such as docks *Rumex sp*.. Grasses, sedges, mosses and less palatable species such as bracken *Pteridium sp.* tend to dominate under heavy grazing (Gill and Fuller 2007, Nuttle et al. 2014). Herbivory tends to accelerate succession from an open scrub-like state to closed woodland canopies with reduced shrub and ground layers (Joys et al. 2004). However, ecosystems are dynamic and species composition changes over time in response to factors in addition to herbivory, including storms, woodland management, and soil acidification (Brunet et al. 1996, Kirby 2001).

Table 1-1. The impact of increased grazing intensity on woodland biodiversity, taken from Mitchell & Kirby (1990).

Component	**No grazing → High intensity grazing**					
Trees & Shrubs	No regeneration due to competition from dense ground vegetation	Creation of regeneration niches	Loss of seedlings and damage to saplings	Loss of saplings and severe tree browsing	Barking of mature trees and loss of shrub layer	Creation of parkland or moorland
Higher plants	Reduced diversity dominated by a few vigorous species	Reduction in vigorous species, and an increase in diversity	Reduction in vegetation structure and an increase in grazing tolerant species	Loss of plant diversity, particularly of grazing sensitive species	Loss of cover and damage due to trampling. Bare ground patches	Impoverishment due to net loss of nutrients from the system
Lower plants	Reduced cover and diversity due to competition from higher plants	Increase in cover of ground dwelling species as competition from higher plants is reduced		Damage to ground dwelling species due to trampling	Reduction of drought sensitive bryophytes	Increase in epiphytic lichens associated with parkland
Invertebrates	High populations of phytophilous species	Increase in diversity as sward structure diversifies	Increase in dung-utilising species	Decline in woodland species		Increase in parkland/moorland species
Birds	Favouring birds of dense shrub layers	Increase in diversity as structural diversity increases	Increase in species favouring low shrub cover	Loss of ground nesting birds due to poor concealment	Loss of species dependent on berry-bearing shrubs	Reduction in raptors dependent upon small mammals

In the short-term, it is the shrub layer which is most affected by herbivory; browsing by deer reduces the density and abundance of sapling trees, shrubs and climbers in this habitat (Joys et al. 2004, Gill and Fuller 2007). However, in the long-term, the successional trajectories and the future canopy layer of woodlands can be affected (Côté et al. 2004, Tanentzap et al. 2011, Newson et al. 2012). Such impacts are less studied than the short-term impacts on the shrub and ground layers as they are not observed immediately following browsing – it may take decades before impacts upon canopies are felt. However, studies of the regeneration of tree species in response to browsing provide some insight into potential future changes in species composition in woodlands. Repeated browsing of young trees has been shown to slow down and alter the growth of trees, especially during their first few years of growth (Putman et al. 1989, Welch et al. 1991, Welch et al. 1992, Cooke and Lakhani 1996, Palmer and Truscott 2003, Joys et al. 2004). Regeneration may also be affected through the consumption of seeds or by the reduction of seedling density (Gill 2000, Gill and Morgan 2010, Akashi et al. 2011, Putman et al. 2011a).

Despite the fact that apparent preferences of deer for different plant species have been documented (e.g. Gill 1992a, Cooke and Farrell 2001), conflicting accounts of the palatability of individual plant species are sometimes found. This can make it difficult to compare results between studies given that preferences in one habitat may not apply in another (Gill 1992a). Despite this, it is clear that some plant species, such as ivy *Hedra helix*, honeysuckle *Lonicera periclymenum* and bramble *Rubus fruticosus* are almost universally favoured and "*form a very important component of the diet [of British deer], particularly in winter*" (Gill and Fuller 2007). Indeed, the availability of bramble has been suggested to control the carrying capacity of deer (Cooke and Farrell 2001). Conversely, some plant species benefit from browsing (of competitors) due to their unpalatablility, or because they are tolerant to browsing (Cooke and Farrell 2001). Examples include many grasses (Baines et al. 1994, Corney et al. 2008), ferns, and few flowering plants such as ground ivy *Glechoma hederacea* (see Cooke and Farrell 2001).

Although many negative impacts of deer herbivory have been recorded, browsing and grazing by deer can have beneficial effects. For example, many land-managers of heathland regard deer browsing as an important tool in the prevention of scrub

regeneration (Rosie Rowe, Defence Estates deer operations manager, *pers comm*.). Deer may also facilitate the spread of plant species by dispersing viable seeds in faeces (Gill and Beardall 2001, Gill and Fuller 2007), with grazing species tending to disperse more seeds than browsing species; grazing red and fallow deer in Thetford Forest deposited significantly more seed species than sympatric, concentrate-selecting roe and muntjac deer, despite having smaller populations (Eycott et al. 2007).

Aside from grazing and browsing, deer may affect vegetation through activities such as bark stripping, trampling, and by fraying, which is caused by rubbing antlers against trees to clear antlers of velvet, as an aggressive display, or to scent mark (Gill 1992a). Physical impacts resulting from fraying and bark stripping weaken trees by exposing them to fungal infection and desiccation, and can also affect the respiration and photosynthesis of the tree, occasionally causing its death (Ratcliffe 1989, Gill 1992a). Deer may also affect soil nitrogen availability, and therefore plant productivity, by affecting feedbacks between plants and soil microbes, and through deposition of urine and dung (Harrison and Bardgett 2004, Gill and Fuller 2007).

It is clear that deer impact on vegetation in a number of ways and that these changes almost certainly have cascading impacts upon other components of the ecosystems they inhabit. For example, if deer reduce the diversity of shrubs and saplings (Gill and Beardall 2001) this may, in turn, affect the number and diversity of invertebrates, which could affect food resources for insectivorous birds (e.g. Holt et al. 2010). Indeed, a number of studies have shown a relationship between an increase in deer abundance and a decrease in the abundance (Degraaf et al. 1991, deCalesta 1994, McShea and Rappole 2000, Perrins and Overall 2001, Allombert et al. 2005a, Gill and Fuller 2007, Baiser et al. 2008) or diversity (Casey and Hein 1983) of birds. Changing vegetation structure is the principal mechanism by which deer impact on bird abundance and community composition, by altering the available habitat for birds to forage and/or nest as well as increasing their exposure to predators (Martin and Joron 2003, Allombert et al. 2005a, Gill and Fuller 2007). However, other impacts such as direct predation by deer and nest-trampling (Pietz and Granfors 2000), the alteration of food resources (Holt et al. 2010) and alteration of tree species composition can also affect bird communities. Research in these areas has been limited, and is still rather speculative (Fuller 2001).

As Gill & Fuller (2007) discuss, evidence for the effect of deer on birds has been obtained from both natural (e.g. Allombert et al. 2005a, Cardinal et al. 2012) and designed experiments (e.g. Casey and Hein 1983, deCalesta 1994), as well as from circumstantial evidence (e.g. Fuller 2001, Perrins and Overall 2001, Gill and Fuller 2007). Much focus has been on multi-deer environments (e.g. Casey and Hein 1983, Gill and Fuller 2007, Holt et al. 2010) rather than focussing on the impact of one species of deer [but see studies of white-tailed deer (deCalesta 1994, Rooney and Waller 2003, Cardinal et al. 2012) and Sitka-black tailed deer (Martin et al. 2010) in America]. More research is required to ascertain the interaction between deer density and bird density (Fuller 2001) in order to provide more successful deer management options for the benefit of birds.

Numerous studies have provided evidence that heavy grazing and browsing by deer reduces species richness (Fuller and Gill 2001). However, studies have generally focused upon impacts on a single species, guild, or taxon. Multi-trophic approaches at the same sites have been advocated (Stewart 2001) to gain a deeper insight into the effects of deer on biodiversity. Research focusing on the effects of varying levels of herbivory by different species of deer has been advocated (Feber et al. 2001, Benes et al. 2006), given their differences in body size, habitat use and feeding preferences (Putman 2003, Putman et al. 2011a). Furthermore, the majority of studies investigating impacts have been undertaken using exclosure or artificial-stocking experiments (e.g. Ballon et al. 1992, Baines et al. 1994, Cooke et al. 1995, Cooke 1997, McShea and Rappole 2000, Morecroft et al. 2001, Stone et al. 2004, Kleintjes Neff et al. 2007), which do not always reflect what would occur under natural conditions (Allombert et al. 2005a). Therefore, it is suggested that impacts should be investigated across sites with a range of deer densities (Fuller and Gill 2001); Fuller (2001) suggests that "*the most valuable approach would identify how species are distributed across a gradient of grazing pressure within the same broad type of woodland and how deer affect the availability of critical resources for ...[species]... across this gradient*."

The scope of this thesis is limited to investigating the observed effects of deer on their environment (Chapters 5 and 6), rather than predictions of their effects given the difficultly and uncertainty associated with doing so (Tanentzap et al. 2013). Indeed, despite the wealth of studies that document the effects of herbivores on their

environment, projections of how vegetation may change in the future in response to this pressure are scarce. Predictive browse models (e.g. Holland et al. 2013, Tanentzap et al. 2013) are likely to become an important management tool, highlighting the potential implications of increases in herbivore abundance and quantifying how different herbivore and vegetation management strategies will shape woodlands in the future. A first attempt to create spatially explicit predictions of the impacts of herbivores on vegetation at a landscape scale used data on the distribution of young trees in a 40km^2 nature reserve, and simulated the growth, dispersal, recruitment and mortality of these trees in response to varying levels of herbivory by red deer (Tanentzap et al. 2013). Tanentzap and co-workers (2013) study corroborated the findings of experimental studies – at high deer densities regeneration and expansion of trees is restricted – but the authors were also able to state explicitly how management could be used to encourage future tree regeneration. They found that management of deer alone would not increase the density of trees in the short-term (<30 years); an increase in ground cover, which facilitates establishment, would also be required for birch regeneration (Tanentzap et al. 2013). Where deer numbers are low, woodland management to promote shrub re-growth can mitigate against the impacts of deer presence (Fuller et al. 2007). Such measures include thinning, selective felling, or using deer-proof fences to protect young vegetation from deer herbivory (Fuller and Henderson 1992). However, when deer densities are high, managing their impacts becomes more difficult, and predictive models such as those used by Tanentzap *et al.* (2013) are likely to become increasingly important tools for aiding deer management.

1.5. The distribution and ecology of British deer

In the first part of this section, I present the information on the current distribution and abundance of deer in Britain, which will be referred to in my species distribution modelling chapters (Chapters 2 to 4). I also provide a brief overview of the habitat use, diet, social organisation and body size of British deer as the characteristics of damage caused by these species vary due to differences these aspects of their ecology (Putman 2003, Putman et al. 2011a).

There are six species of wild deer in Britain: the native red and European roe deer, the naturalised fallow deer *Dama dama*, and the non-native sika *Cervus nippon*, Chinese

muntjac (muntjac) *Muntiacus reevesi*, and Chinese water deer (CWD) *Hydropotes inermis*. Fallow deer were present in Britain during the last interglacial period, and were then reintroduced to Britain during the 11th century; the three non-native species were introduced to Britain just over 100 years ago (Ward 2005).

1.5.1. The origins of British deer

Red and roe deer are native to Britain. Red deer occur in the fossil record from the mid-Pleistocence approximately 400,000 years b.p. and roe deer have been present in Britain since approximately 10,000 years b.p. (Corbet and Harris 1991, British Deer Society 2010e). The abundance of both species was greatly reduced across Britain in the 18th century as a result of extensive forest clearance and over-hunting (Corbet and Harris 1991, Ward 2005, British Deer Society 2010e). Local extinctions of both species occurred in England, Wales and the Scottish lowlands, leaving only small populations of both species in the Scottish uplands and of red deer in southern England (Corbet and Harris 1991, Prior 1995, British Deer Society 2010e, d). In recent centuries, populations of both species have grown due to the introduction of both native and non-native stock, and, in the case of red deer, escapes from deer parks (Whitehead 1964, Corbet and Harris 1991, Prior 1995, Staines et al. 1998, British Deer Society 2010d, Baker 2011).

Fallow deer were present in the U.K. over 400,000 years ago but went extinct during the last glaciation (Chapman and Chapman 1980, Corbet and Harris 1991), which ended around 12,500 years ago. The current populations of fallow deer apparently originate from introductions to Britain by the Normans for hunting purposes in the 11th century (Chapman and Chapman 1980, Corbet and Harris 1991, Ward 2005). Many deer parks were established for fallow deer during Mediaeval times and by the middle of the 17th century there were over 700 deer parks in England (Harris et al. 1995, Perez-Espona et al. 2009). However, by 1988, that number had reduced to 120 (Harris et al. 1995).

Sika deer are native to Japan and adjacent parts of Korea and China. Several sub-species were released into Britain but Japanese sika *C. n. nippon* are the only subspecies known to have become established in the wild (Ratcliffe 1987). The first sika deer in the British Isles included one stag and three hinds introduced at

Powerscourt, Dublin in 1860 (Corbet and Harris 1991, Harris et al. 1995, British Deer Society 2010f); approximately 50 additional introductions (of unknown numbers) occurred across Britain from then onwards (Ratcliffe 1987).

Both Chinese muntjac and Indian muntjac *M. muntjac* were introduced into Woburn Park, Bedfordshire around 1894 but little is known about how many deer, or how often, they were imported (Chapman et al. 1994). Indian muntjac did not establish themselves in the wild and those within the park were killed to make way for more Chinese muntjac (Corbet and Harris 1991, Staines et al. 1998). Chinese muntjac subsequently escaped and were released into the wild, and are now the only species of muntjac in the wild in Britain (Corbet and Harris 1991, Yalden 1999).

Chinese water deer (CWD) were introduced to Whipsnade Zoo in Bedfordshire in 1929 (Corbet and Harris 1991). Approximately ten years later, some of these individuals (and their descendants) were taken to Woburn Park, Bedfordshire and to two locations in Hampshire; they were subsequently reported to escape from all four locations (Yalden 1999). Additional escapes and releases from deer parks has meant that this species has become established in the wild in Britain (Corbet and Harris 1991). However, CWD are classed as vulnerable by the IUCN, with populations in their native China and Korea in decline as a result of habitat destruction and poaching (www.iucnredlist.org/details/10329/0, accessed 13th July 2013).

1.5.2. The present-day distribution of British deer

The most widely distributed and abundant deer species in Britain is the roe deer (Staines et al. 1998, British Deer Society 2010e). They are currently found throughout Scotland and across the majority of England (Figure 1-2) (Ward 2005) but are expanding, filling the gaps in their British distribution (Putman and Moore 1998). Red deer are most numerous in Scotland but there are isolated populations throughout England and Wales (Figure 1-2). In the last decade, their range has expanded most noticeably in East Anglia and the midlands.

Fallow deer are relatively widespread in England and Wales but are only patchily distributed in the southern areas of Scotland (British Deer Society 2010b) (Figure 1-2). Staines et al. (1998) state that fallow "*have tended to remain in the vicinity of their*

release or escape sites"; the recent increase in feral fallow deer appears to have resulted from escapes from deer parks (Chapman and Chapman 1980, Harris et al. 1995).

Sika deer are currently relatively widespread in Scotland (British Deer Society 2010f), which has been attributed to the presence of newly maturing conifer plantations (Yalden 1999) which they use for both food and cover. In England, populations are patchily distributed in Cumbria, Hampshire, Lancashire, Northamptonshire, Dorset and Bedfordshire (Figure 1-2) (Harris et al. 1995).

Muntjac range expansion in the past decade has been particularly rapid, especially westwards into central England (Figure 1-2). This rapid spread across England and Wales has been attributed to artificial translocation by humans (Chapman et al. 1994, Ward 2005, British Deer Society 2010c). Wild muntjac were initially found in areas where fallow deer were the only other deer species, but have since spread into areas where roe deer are the most common deer species (Staines *et al.* 1998), resulting in increased competition between the native roe and non-native muntjac (e.g. Hemami et al. 2004, Hemami et al. 2005).

CWD have established only small populations in Britain at present, centred around their release and/or escape sites (British Deer Society 2010a). One population has established itself in Woodwalton Fen, Cambridgeshire and other populations occur on the Norfolk Broads (Yalden 1999) and in Bedfordshire, while additional sightings have been recorded at isolated locations across Britain (Figure 1-2). Occupied areas tend to be fens, which provide habitat similar to those in their native range (Corbet and Harris 1991, British Deer Society 2010a). This species is the least numerous and most geographically limited of the wild British deer species (Figure 1-2); presumably, numbers are limited by the comparatively small area of suitable habitat in Britain.

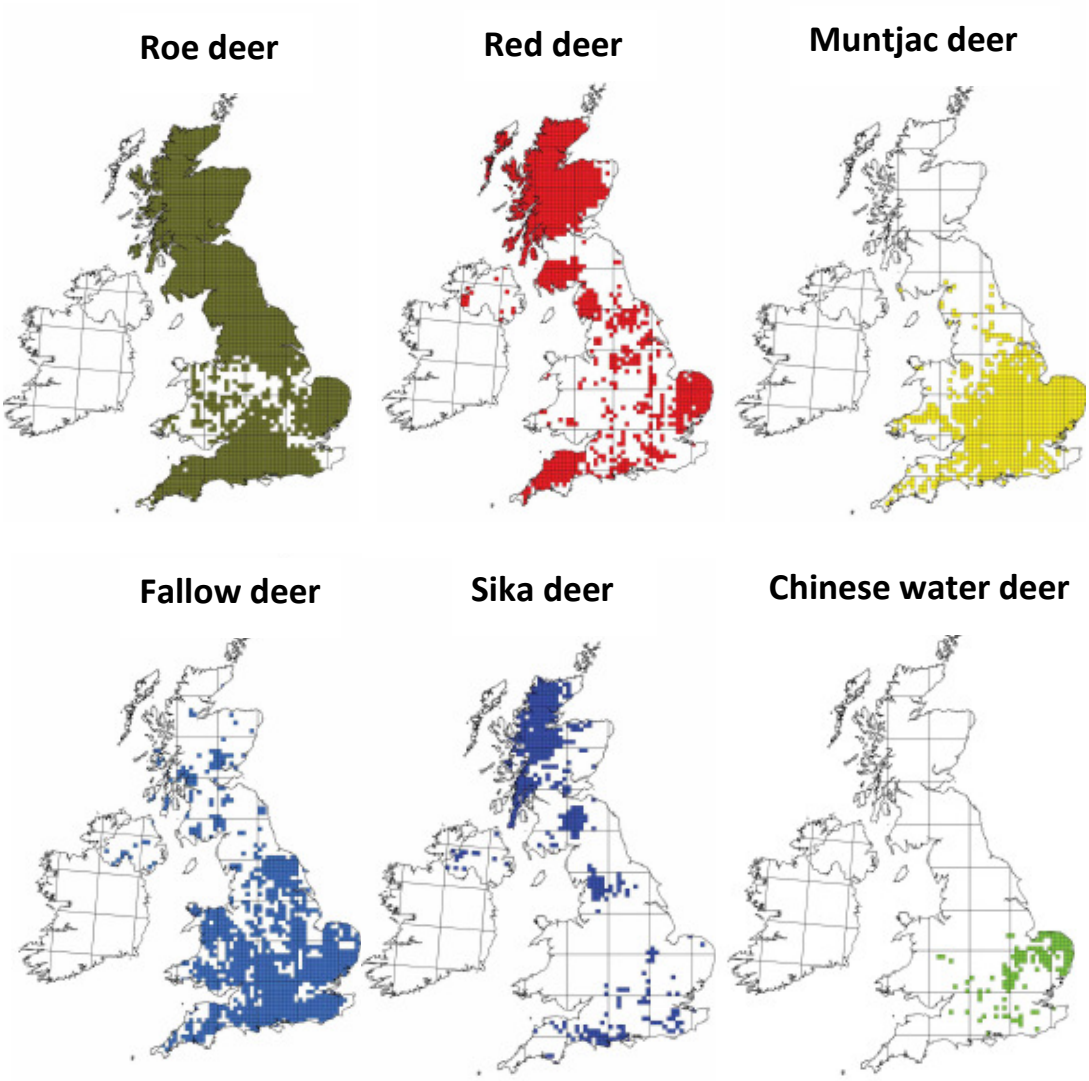


Figure 1-2. Distribution of roe, red, muntjac, fallow, sika and Chinese water deer in Great Britain and Ireland in 2007 (taken from www.bds.org.uk/deer_distribution, accessed December 2009). Coloured squares indicate species' presence in the corresponding 10km^2 national grid square.

1.5.1. Recent changes in range and abundance

While presence/absence distribution maps for these species are available for a number of different time periods (e.g. Arnold 1984, Corbet and Harris 1991, Arnold 1992), only two studies have quantified recent range expansion for all six species (Ward 2005, Ward et al. 2008) (Table 1-2). The ranges of all species have increased particularly rapidly during the last decade. Recent range expansion of the CWD is most marked, at 22% per annum (Ward et al. 2008) but they remain the most geographically restricted and least abundant deer species in the wild in Britain (Table 1-3, Figure 1-2).

Although some estimates of deer abundance are available for individual sites (such as nature reserves and private estates), there are only three published estimates of the abundance of deer across the whole of Britain (Table 1-3) (Putman and Moore 1998).

Table 1-2. Annual range expansion of the six deer species across Britain. Values are taken from Ward (2005) and Ward *et al.* (2008). Compound annual increase is calculated using Equation 1-a, below (Ward, *pers. comm.*).

	Compound annual increase in range (%)	
Species	1972 - 2002	2002 - 2007
Chinese water deer	2.0	22.2
Chinese muntjac	8.2	11.6
Fallow deer	1.8	12.5
Red deer	0.3	7.3
Roe deer	2.3	5.2
Sika deer	5.3	7.3

$$Compound\ annual\ increase = (\left(\left(\frac{N_{t+1}}{N_t}\right)^{\left(\frac{1}{y}\right)}\right) - 1) * 100 \qquad \textbf{Equation 1-a.}$$

Where N_{t+1} is the number of occupied grid squares in the most recent period (i.e. 2002 or 2007 in the table above), N_t is the number of occupied cells at the initial survey period (i.e. 1972 or 2002 in the table above), and y is the number of years between the most recent and the initial survey periods.

Table 1-3. Estimated population size (c. 1975, 1995 and 2009) of the six deer species found in the wild in Britain, adapted from Gibbs *et al.* (1975)[a,] Harris *et al.* (1995)[b] and P.O.S.T. (2009)[c].

	1975[a]	1995[b]			2009[c]
Species	England	England	Wales	Scotland	Britain
Chinese water deer	None given	650	0	0	10,000
Chinese muntjac	5,000	40,000	<250	<50	150,000
Fallow	50, 000	95,000	<1,000	<4,000	150,000 – 200,000
Red	190, 000	12,500	<50	347,000	>350,000
Roe	200,000	150,000	50	350,000	800,000
Sika	1,000	<2,500	0	9,000	35,000

Evidently, the abundance of all six species has increased dramatically between 1975 and 2009 – especially the CWD, sika and muntjac deer (Table 1-3). However, the estimates of population size described in Table 1-3 can only be used as a guide to the

magnitude of population change rather than an accurate reflection of numbers (P.O.S.T. 2009), as deer population density is difficult to estimate (Harris et al. 1995, Fuller and Gill 2001, Perrins and Overall 2001).

Major causes of deer mortality include harsh winters, disease, poaching, predation, and deer-vehicle collisions (Harris et al. 1995, P.O.S.T. 2009, Langbein 2011). However, by far the biggest cause of mortality is culling; although nearly 35000 deer are culled annually in Britain, this number will need to be increased if we are to keep populations in check (P.O.S.T. 2009).

1.6. The ecology of British deer

As with other ungulates, the feeding strategies of British deer reflect the choice of food they consume, the habitats they are associated with, and their physiology (Jarman 1974). The six species of British deer can be roughly split into two groups based on their feeding strategies and social organisation, with red, sika and fallow deer in one group, and roe, muntjac and CWD in the other. Red, sika and fallow deer form large herds and are highly mobile, ranging over large areas (Putman et al. 2011a). In general, males and females of these species remain separate throughout the year, with the exception of the rut (throughout September, October and November for all three species) (Corbet and Harris 1991, British Deer Society 2010d, b, f). Males defend groups of females during the rut, while females tend to occupy adjacent and overlapping ranges which they do not defend (Corbet and Harris 1991). These three species tend to be bulk feeders (Putman 2003), grazing on vegetation which is of poor quality, particularly grasses (Bullock 2009). Fallow deer prefer mature broadleaved woodland with dense shrub-layer vegetation, but are often found grazing on agricultural crops (Corbet and Harris 1991, British Deer Society 2010b). Historically, red deer were woodland species, and will therefore occupy woodlands where possible (Holmes 1974, Corbet and Harris 1991). However, "*the greatest concentrations [of red deer are] found on open moorland of the Scottish Highlands and Islands*" (Corbet and Harris 1991). Conversely, sika deer are "less able to adapt" to life in open habitats and are therefore, usually found in heathlands interspersed with dense coniferous woodlands (Corbet and Harris 1991, British Deer Society 2010f).

The roe, muntjac and CWD are less social, resident species, which are also selective foragers (Corbet and Harris 1991, Putman 2003). Given their small body size and physiology (Forde 1989), these species select easily digested, high-quality vegetation such as new growth of grasses and tree leaves (Bullock 2009). Shoots of *Rubus* species are the main component of their diet, but they also eat many other plants including ivy, grasses, root vegetables and the shoots of broadleaved trees such as beech *Fagus sylvatica* and holly *Ilex aquifolium* (Corbet and Harris 1991). These species are usually solitary or found in pairs of either mating male and female, or a female and offspring (Corbet and Harris 1991, British Deer Society 2010e, c, a). The home ranges of females sometimes overlap, but individual core ranges are exclusive (Putman 2003). Males aggressively defend their territory from other males during the rut (British Deer Society 2010c, e), which occurs during July and August for roe deer (British Deer Society 2010e), and during November and December for CWD (Putman 2003). Unlike the other deer species found in Britain, muntjac are not entrained to an annual breeding cycle (Chapman et al. 1997), so there is no obvious peak in number of births at a given time of the year (Corbet and Harris 1991).

Roe deer are associated with deciduous or open coniferous woodland, occurring at high densities in young woodlands (Corbet and Harris 1991, Harris et al. 1995, Radeloff et al. 1999). As in their native China, CWD are associated with broadleaved woodlands and wet habitats, but they also venture onto agricultural land for food during the autumn and winter (British Deer Society 2010a). Muntjac prefer forested areas with dense and diverse understorey vegetation, but are increasingly being found in urban areas in locations such as railway embankments and residential gardens (Corbet and Harris 1991, British Deer Society 2010c).

Further details on the demographic characteristics of British deer – required to parameterise population models in Chapters 3 and 4 – are provided in Appendix 2.

1.7. The influence of diet on ecological impacts

An overview of impacts of deer on their environment has been provided earlier in this chapter, and is discussed in further detail in the introductions of Chapters 5 and 6. Here I provide a brief overview of impacts relating to the two species groupings

defined above, as it has been suggested that the severity and style of impacts are equivalent within these groups (Putman et al. 2011a).

The large-bodied red, sika and fallow deer form large herds and range over large areas (Putman 2003, Putman et al. 2011a). Consequently, impacts of browsing within woodlands and grasslands are irregular, but can be substantial (Corbet and Harris 1991, Putman 2003). These species can prevent the regeneration of coppice, reduce yields of commercial forestry and the affect the conservation of native woodlands (Corbet and Harris 1991). Additionally, all three species will strip and sometimes fray the bark from trees (Gill 1992a), inhibiting their growth.

The less social, resident species (muntjac, roe and CWD), create a constant, sustained impact on the habitats where they reside (Putman 2003). As concentrate selectors (Putman 2003), the impacts of their feeding tend to be quite localised. Muntjac and roe deer have been known to prevent the regeneration and establishment of woodlands and re-growth of coppice, given their tendency to browse on the growing shoots of trees (Corbet and Harris 1991, Putman and Moore 1998). Muntjac were previously considered to have negligible impacts on British wildlife (as discussed by Ward 2005) but several papers now describe their negative influence (e.g. Pollard and Cooke 1994, Ward 2005, Hemami et al. 2007). The CWD is currently thought to cause negligible impacts (Ward 2005, British Deer Society 2010a). However, given that it is very little studied in the U.K., its impact on native fauna and flora remains to be quantified (Ward 2005).

1.8. Thesis structure and aims

The remainder of the thesis is split into two main sections. In the first section (Chapters 2 to 4) I use a combination of correlative and mechanistic modelling approaches to predict how the distribution of deer may change in in the future. Specifically, in Chapter 2, I use static, correlative models to describe habitat suitability for species that are currently expanding their ranges by accounting for the fact that species are not at equilibrium with their environments. I compare the spatial extent of environmentally suitability areas predicted using this modelling approach to those predicted by two other, commonly used methods.

In Chapter 3 I develop a spatially explicit population model (SEPM) which can be used to predict the pattern and rate of spread of organisms across a heterogeneous environment. I validate the SEPM by retrodicting the spread of roe, red and muntjac deer in Britain between 1972 and 2007. I also use the SEPM to determine the effect of varying key demographic variables on the spread of deer.

In Chapter 4 I use the SEPM to predict the potential future distribution of roe, red and muntjac deer in Britain. This is the first attempt to predict the future distribution of deer at a national scale using a spatially-explicit mechanistic model. I discuss differences in the predicted distributions created using SEPMS, to those using the correlative modelling approach developed in Chapter 2, and highlight the importance of incorporating species-specific traits in predictive distribution models. I also investigate the influence of key life-history parameters on the spread of deer.

In the second section of this thesis (Chapters 5 and 6) I investigate the impact deer have on their environment. Specifically, in Chapter 5 I use data collected from 35 field sites across Britain to investigate the relationships between roe deer density and woodland habitat structure, vegetation diversity, density and species composition.

In Chapter 6 I explore the cascading effects of herbivorous ungulates by investigating the relationships between changes in deer density and changes in bird abundance. The focus on the contrasting fates in the temporal trends of two sympatric groups of bird species – those classed as either sensitive or tolerant to herbivory by ungulates – provides a unique and robust approach to quantifying the cascading effects of keystone species. Finally, in Chapter 7 I bring together the findings of this thesis and provide a general discussion.

Chapter 2 : Modelling habitat suitability for species with expanding ranges

2.1. Abstract

Background: Correlative species' distribution models (SDMs) are often used to predict environmental suitability for species, but assume that species are at equilibrium with their environment; for species with expanding ranges, this assumption is violated. Here, I develop and test a novel method to predict habitat suitability for expanding-range species.

Methodology: Roe deer *Capreolus capreolus*, red deer *Cervus elaphus,* and Reeves' muntjac deer *Muntiacus reevesi* abundance data were obtained from the British Trust for Ornithology's Breeding Bird Survey Scheme, and presence/absence data from surveys carried out by the British Deer Society. Habitat suitability was estimated by relating abundance data within each species' observed range extent (i.e. where it was assumed to be at equilibrium with their environment) to land-cover variables, obtained from satellite imaging. Predicted habitat suitability values using this approach were compared to those obtained using presence-only and presence/absence data.

Findings: All three modelling approaches were comparable in terms of describing the observed distribution of species (AUC for abundance, presence-absence and presence-only models for the three species ranged between 0.50 and 0.64). However, for muntjac and red deer, the abundance models predicted larger areas of suitable habitat across unoccupied parts of the UK than the other modelling approaches. In particular, the non-native muntjac deer are likely to expand their range into northern England and southern Scotland to a much greater extent using models incorporating abundance data than those using presence-only or presence/absence data.

Conclusions: The abundance-modelling methodology described here likely provides a better reflection of potential ranges of species which are expanding their range. The outputs from these models can be incorporated into mechanistic models (Chapter 3) – which account for range limiting processes – in order to create more realistic predictions of the potential future distribution of range-expanding species.

2.2. Introduction

Predicting species' range changes due to habitat or climate change is important for planning their conservation and management. Species' distribution models (SDMs), describing the relationship between species and their environment, have been used for such applications (e.g. Beerling et al. 1995, Peterson et al. 2003, Richardson and Thuiller 2007, Ficetola et al. 2010, Giljohann et al. 2011). A key assumption of SDMs is that species are at equilibrium with their environment, occupying all suitable areas of habitat and absent from all areas of unsuitable habitat (Guisan and Zimmermann 2000, De Marco et al. 2008, Zurell et al. 2009). This assumption is particularly problematic for species with expanding ranges because a species may be absent from an area simply because it has not yet reached that location, not necessarily because the area is unsuitable (Jarnevich and Reynolds 2011, Gasso et al. 2012).

Predictions of environmental suitability for species with expanding ranges are required so that management can be focussed in appropriate locations beyond observed ranges. However, non-equilibrium relationships with environmental conditions pose serious challenges for deciding which modelling approaches or datasets are most appropriate, and for determining how best to evaluate model performance (Elith et al. 2010). Much focus has been on the use of different modelling techniques, including the relative merits of using either presence/absence or presence-only data (Elith et al. 2006, Hijmans and Graham 2006, Pearson et al. 2006, Elith et al. 2010). Despite suggestions that models using abundance data would be an improvement on those using either presence/absence or presence-only data, abundance data are rarely used to model environmental suitability (Pearce and Boyce 2006, Elith and Leathwick 2009), and comparisons between these three modelling approaches are lacking.

Problems associated with modelling non-equilibrium distributions are highly relevant for cervids, given that their populations have been increasing in abundance and range across the world over recent decades (Côté et al. 2004, Dolman and Waber 2008). British deer are no exception: their range sizes have increased by up to 22% annually, and are expected to continue to expand (Table 1-2) (Ward 2005, Ward et al. 2008). Such populations potentially threaten agricultural crops, forestry, horticulture and protected habitats as well as other taxa, including humans (Putman and Moore 1998,

Côté et al. 2004, Vila et al. 2009). Here, I focus on British deer to explore the importance of the type of input data in identifying habitat suitability for expanding-range species. While Acevedo *et al.* (2010) and Chapman *et al.* (1994) have described environmental suitability for deer at a landscape scale across Britain (and Pompilio and Meriggi 2001 for red and roe deer in Italy), these studies used presence/absence data and a large number of predictors in their models, and model performance was tested using non-independent data. Acevedo *et al.* (2010) also used spatial (latitude/longitude) variables, which limit application of the models beyond the observed (current) range of a species.

My specific objectives were to: (1) develop models to predict habitat suitability for three deer species (the native red deer and roe deer, and the non-native Chinese muntjac deer) across Great Britain, using abundance rather than range extent data, and using models un-constrained by the inclusion of spatial predictors; (2) contrast the ability of abundance-based models to predict recent range changes of deer with models using presence-(pseudo)absence or presence-only range data; and (3) compare projections of habitat suitability for the three focal species beyond the species' current ranges.

2.3. Methods

2.3.1. Species data

Deer abundance data

Deer count data were collected as part of the British Trust for Ornithology's Breeding Bird Survey (BBS) monitoring scheme as a measure of relative abundance. These data cover 4561 sites (1km^2 squares) across Great Britain and span the period 1995-2009 (though not all sites have data for each year). Random 1km^2 squares across Britain are surveyed twice per year between April and June. At each visit, counts of birds and mammals along two *c.*1km transects are recorded (Newson et al. 2012). The resultant deer count data correlate well with deer density estimates collected using more labour-intensive methods (Newson et al. 2012).

As CWD and sika deer have restricted distributions in the UK (Figure 1-2) and are also poorly monitored by the BBS [CWD were recorded in 20 sites and sika in 61 sites across

the U.K. between 1994 and 2009 (Wright et al. 2009 in Newson et al. 2012)], they were excluded from the analyses in this, and later, distribution modelling chapters. Fallow deer were excluded from the species-distribution-modelling chapters as they "*have tended to remain in the vicinity of their release or escape sites*" (Staines et al. 1998) (Chapman and Chapman 1980, Harris et al. 1995). As such habitat associations would be an artefact of where deer parks were/are located, rather than true preferences for a given habitat(s).

Deer presence/absence data

Data for roe, red and muntjac deer presence at 10km^2 and 1km^2 resolutions between the years 1973 and 2007 were downloaded from the National Biodiversity Network (NBN; available from data.nbn.org.uk), and augmented by observations collected on an *ad hoc* basis by members of the British Deer Society, at a 10km^2 resolution. Deer data from both sources at a 10km^2 resolution for the period 1973 – 2002 were collated to represent the extent of occurrence of deer in 2002, while data from 2003 – 2007 were collated to represent extent of occurrence in 2007 (Figure 2-1). Collating multiple years was necessary to allow for limited census coverage in individual years. Furthermore, these two groupings are in line with previous studies (Ward 2005, Ward et al. 2008). The presence data from the NBN at a 1km^2 resolution were reserved for independent testing of the models.

The BDS presence/pseudo-absence dataset for each species in 2002 (Figure 2-1) was buffered by 10km to define an area (hereafter, the training polygon of each species) within the dispersal capability of each species; a 10km buffer was chosen because mean dispersal distances are of this magnitude (Debeffe et al. 2012). Species occurrences within cells inside the training polygon were assumed to reflect genuine preferences for those environmental types found within the range (i.e. where species were assumed to be at equilibrium with their environment). I used abundance data from those BBS sites that fell within a species' training polygon, resulting in 1552 sites for roe deer, 617 for muntjac and 381 for red deer. These areas provided 12274, 5102 and 2818 site-year records for the three species, respectively.

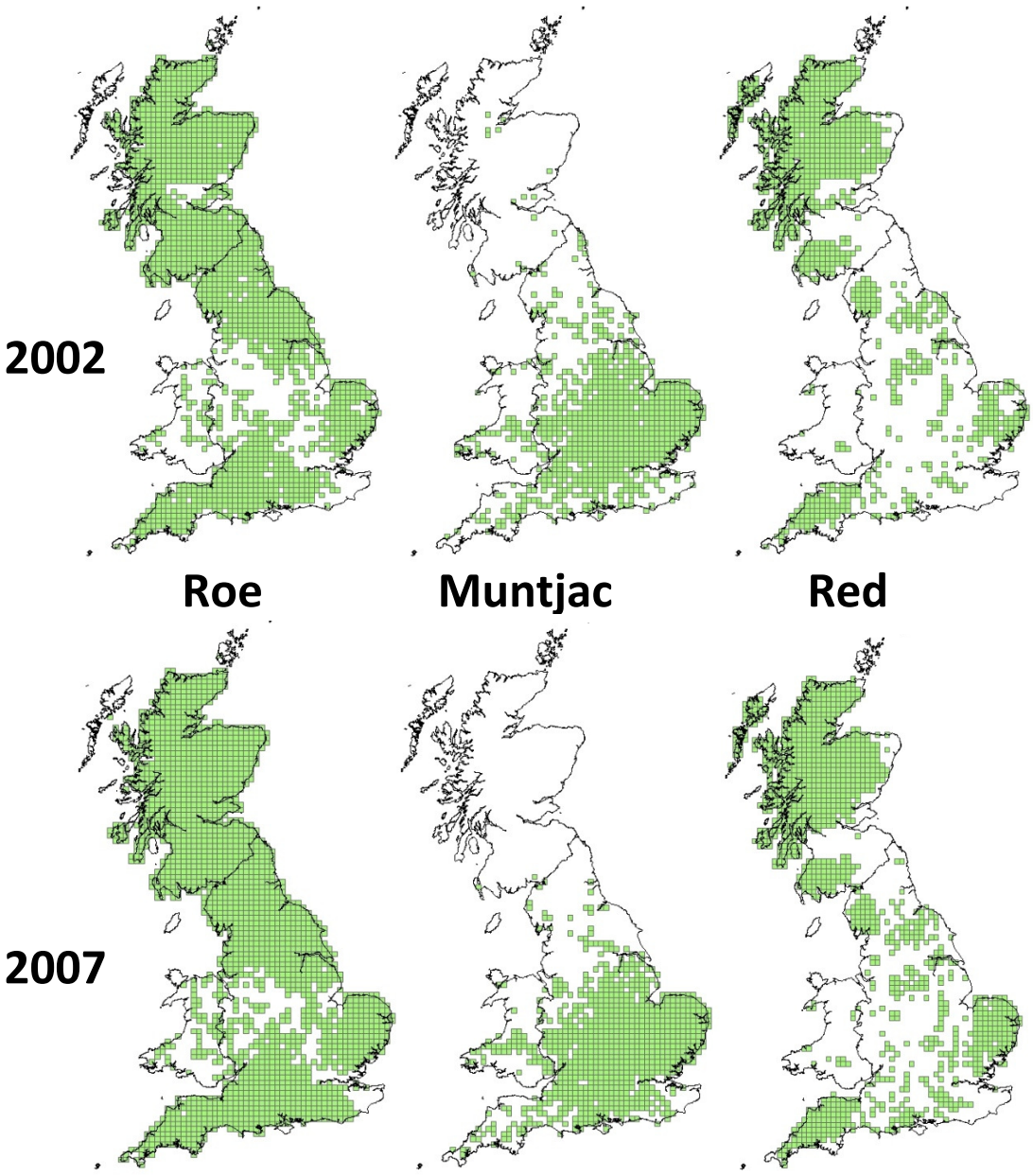


Figure 2-1. Observed distributions of roe deer, muntjac deer and red deer in Britain in 2002 and 2007, obtained from the British Deer Society and the National Biodiversity Network (see '*Deer presence/absence data'* above). Green squares represent species' presence in a 10km^2 cell.

2.3.2. Predictor variables

Land-use (percentage cover) data at a 1km^2 resolution across Great Britain were obtained from the Centre for Ecology and Hydrology's Land Cover Map 2000 (www.ceh.ac.uk/LandCoverMap2000.html). These are derived from remotely-sensed data, and classify land use in Great Britain into ten aggregate classes, eight of which were used as habitat predictors in the models (coastal and oceanic seas were

excluded). These predictors were: broadleaved/mixed woodland; coniferous woodland; arable and horticulture; improved grassland; semi-natural/rough grass and bracken; mountain, heath, bog; built-up areas and gardens; and standing open water and canals. These habitat classes were selected as they have biologically-meaningful effects on deer species' distributions in Great Britain, and have previously been used in habitat suitability models for our focal species (see Acevedo et al. 2010).

2.3.3. Modelling procedures

Models were built for each species using the three species data types (presence-only [BDS data, see page 27], presence/absence [BDS data, see page 27] and abundance data [BBS data, see page 26]). Candidate models ranged in complexity from the null model to models that included all eight habitat predictors as additive terms, as well as a biologically-meaningful interaction between two of the eight habitat variables. Deer counts from 1995 to 2009 were the response variable in the abundance models while, for the other two approaches, the response was presence (and absence) data from 2002 (the mid-point of the abundance dataset). Year was included as a random effect in the abundance models to control for possible inter-annual variation in deer counts.

Presence/absence models were fitted using the 'glm' function in R (R Core Team 2013), while presence-only models were fitted using the program MAXENT (Phillips et al. 2006; Version 3.3.3k). For the abundance models, zero-inflated negative-binomial generalised linear models with a log link were fitted using the 'glmmADMB' package in R (Skaug et al. 2011, R Core Team 2013). This model structure allowed me to account for the over-dispersed, zero-inflated response variable.

The best models for the presence/absence and the abundance model approaches were selected as those with the lowest Akaike's information criterion (AIC). The best model for the presence-only modelling approach was selected as the model with the highest area under the receiver operating characteristic curve [AUC; MAXENT does not output AIC values and AUC is commonly employed in studies using MAXENT; Phillips *et al.* (2006)].

2.3.4. Model evaluation

The predictive abilities of the best models were assessed using three steps. First, the best model for each species and model type was rebuilt using the data described in *Modelling Procedures*, but excluding 10km^2 cells where there were 1km^2 presence records for each species from the NBN (see *Deer presence/absence data*). Second, the resultant models were used to predict habitat suitability at a 1km^2 resolution across all of the excluded 10km^2 cells. Third, these predictions were compared to the independent dataset of observed presence and absence of deer at a 1km^2 resolution, using the threshold-independent statistic: AUC. AUC scores range between 0 (systematically wrong) and 1 (perfect agreement). There are no guidelines for categorising AUC scores (Gallien et al. 2012), but, for the purposes of this chapter, I was interested in how the AUC scores of each modelling approach compared, rather than in the AUC scores themselves.

The best models for each of the three modelling approaches were used to identify locations across Great Britain, and beyond present-day ranges, which were environmentally suitable for each species. To do this I followed four steps. First, whole of Britain was divided into ten blocks (folds), each with approximately the same number of species' presences (i.e. the same number of observed presences for the presence/pseudo-absence and presence-only approaches, and the same number of BBS sites with abundance data for the abundance-modelling approach). Second, *k*-fold partitioning (Fielding and Bell 1997) was used, which allows for independent validation of the models; each best model was built on *k*-1 folds of the data, and then used to predict habitat suitability in the left-out data fold. Third, the predictions of habitat suitability (with values running between 0 and 1) for the whole of Britain were converted to binary presence/absence using a threshold which maximised the True Skill Statistic (TSS) (Allouche et al. 2006); any prediction below the threshold was termed unsuitable habitat in a given cell, and *vice versa*. Fourth, the number and locality of observed presences and predicted suitable habitat of each species for each modelling approach were compared.

2.4. Results

The best model using abundance data (appendices: Table S1, page 163) was comparable to the presence/pseudo-absence or presence-only best models in predicting the independent 1km^2 presences of each of the three species (see AUC statistics in Table 2-1).

Table 2-1. Performance of the best abundance, presence/absence and presence-only models in predicting the occurrence of roe deer, red deer, and Chinese muntjac deer in a subset of 1km^2 cells across Britain in 2007 (A). Observed and predicted presence and absence of deer across the whole of Britain in 2007 (sum of 10km^2 cells; B) for each of the three modelling approaches is provided.

			Species		
	Performance statistic	Modelling method	Roe	Muntjac	Red
A	AUC	Abundance	0.51	0.61	0.60
		Presence/absence	0.54	0.54	0.64
		Presence only	0.50	0.60	0.58
B	Observed presences		2032	824	1211
	Predicted presences	Abundance	1765	1159	1376
		Presence/absence	971	997	791
		Presence only	1866	881	916

For red deer, models using all three modelling approaches predicted extremely high suitability in the highlands of Scotland, England and Wales (Figure 2-2). However, the abundance models predicted much lower suitability in lowland areas than the other two approaches (Figure 2-2). By contrast, and unsurprisingly, given their wide occurrence in the UK, habitat suitability for roe deer appeared relatively uniform across the country (Figure 2-2). For muntjac deer, predicted suitability was low in the highlands of Scotland but fairly uniform elsewhere, with the exception of a few areas of extremely high predicted suitability around, for example, Thetford Forest in Norfolk and in south-western Scotland (Figure 2-2).

The abundance models predicted highly suitable areas for roe deer beyond their observed range, in the south-west of Wales, eastern East Anglia, and the far south-east of England (Figure 2-2). For muntjac deer, suitable areas beyond the present-day range were predicted in north Wales, north-east England and the lowlands of Scotland (Figure 2-2). For red deer, the model predicted much of Wales, the (eastern) central belt of Scotland and the uplands of northern England to contain suitable habitat, despite absence in these areas at present (Figure 2-2).

Red and muntjac deer were predicted to have larger areas of suitable habitat using the abundance-modelling approach than the presence-only or presence/absence models (Table 2-1). For roe deer, much less suitable habitat was identified by the presence/absence models than by the presence-only and abundance models (Table 2-1). However, in all cases, the total number of predicted presences for roe deer was less than the number of observed presences (Table 2-2) (i.e. all modelling approaches underestimated the range of habitats in which roe deer are found at present). In general, the three focal species were positively associated with coniferous and broadleaved woodland, grassland and arable land, and were negatively associated with urban areas (Table 2-2).

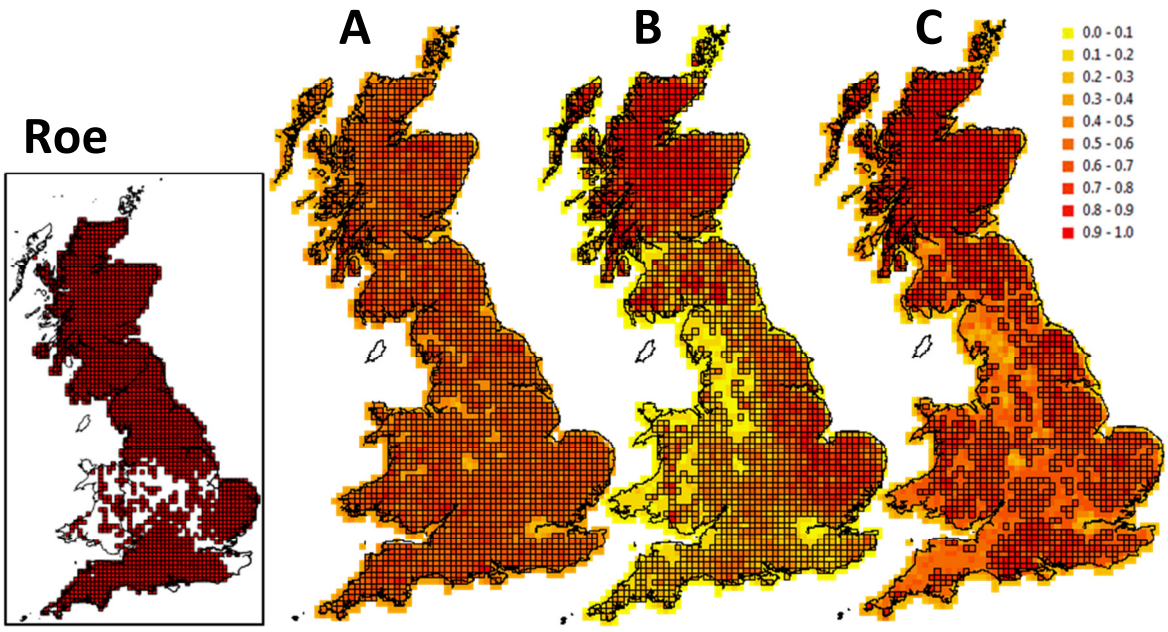


Figure 2-2. Predicted habitat suitability from 10-fold partitioned models (see text) for roe deer, Chinese muntjac deer, and red deer at a 10km^2 resolution across Britain, using abundance models (A, D and G), presence only models (B, E and H), and presence/absence models (C, F and I). Squares with black outlines show predicted presences in 2007 (after applying a threshold to suitability values - see text). Observed presences between in 2007 ('present day') are shown in red on the insert. Figure continued overleaf.

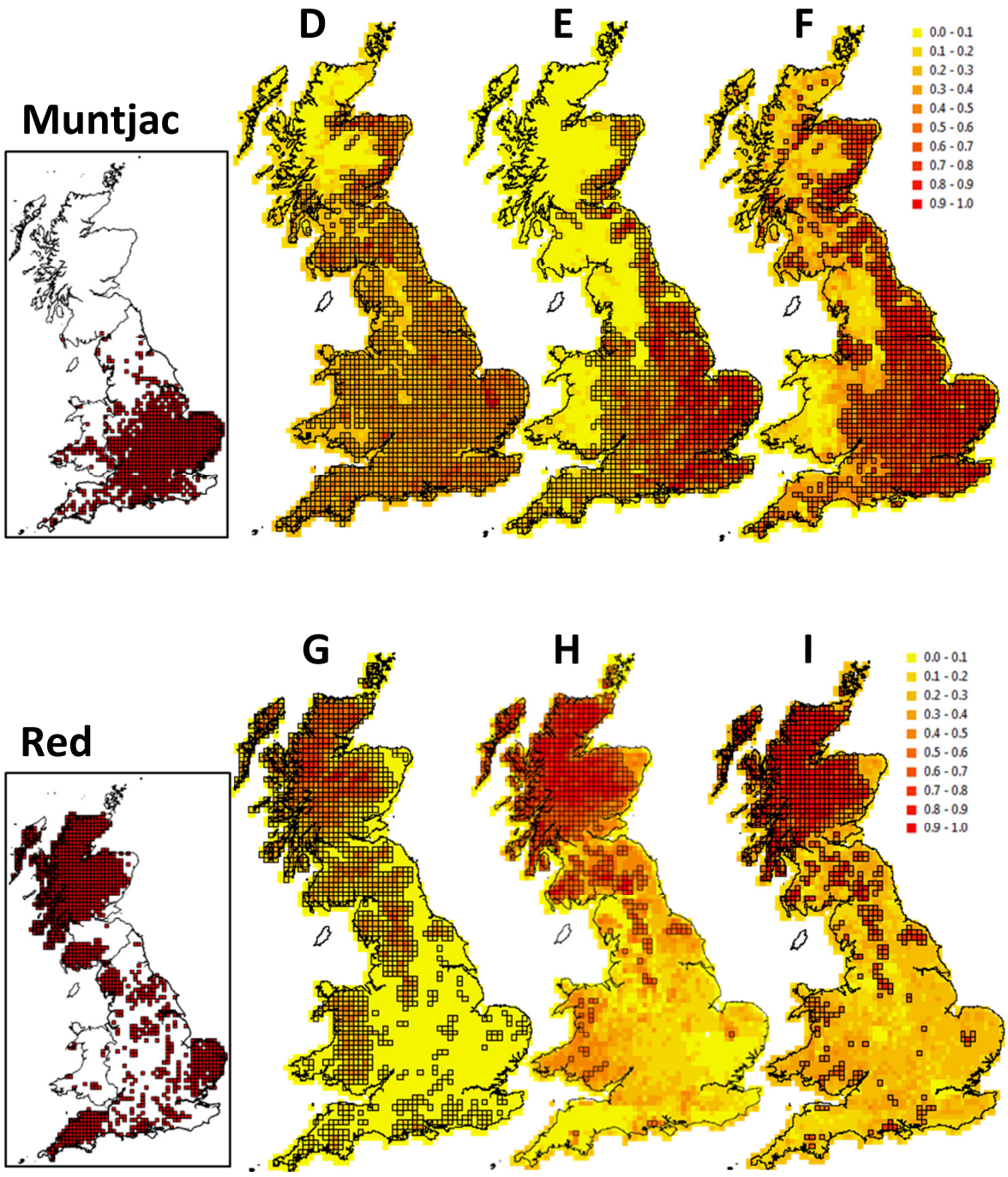


Figure 2-2 cont.

Table 2-2. Model coefficients of variables retained in the best AIC/AUC models predicting habitat suitability across Britain for roe deer, red deer, and Chinese muntjac deer using: deer abundance data (Ab), presence/absence deer distribution data (PA) or presence-only deer distribution data (PO) as the response variables. Significance of each of the PA and Ab model coefficients are shown using symbols shown below the table. The percentage contributions of each of the variables in the PO models are provided in brackets.

		Roe deer			Chinese muntjac deer			Red deer		
Reference	Variable	PA	Ab	PO	PA	Ab	PO	PA	Ab	PO
C1	Broadleaved/mixed woodland	0.04*	1.57*		0.09*	2.08*	2.14 (11.5)	0.02	3.51*	
C2	Coniferous woodland	0.08*	1.23*	1.35 (33.0)	-0.02	1.83*		0.11*	0.68^{+}	-1.31 (9.1)
C3	Arable and horticulture	0.02*	0.72*	0.83 (26.7)	0.03*	0.78*	2.22 (52.3)	0.01*		-0.22 (1.2)
C4	Improved grassland	0.01*	0.81*		0.01			-0.01$^{\$}$		0.02 (0.0)
C5	Semi-natural/rough grass and bracken	0.01			0.01	0.82^		0.01	2.12*	
C6	Mountain, heath, bog	0.04*	1.15*	0.95 (40.7)	-0.04*	-3.60^	-3.97 (28.9)	0.04*	2.69*	-2.42 (89.3)
C7	Built-up areas and gardens		-0.50^{+}		0.03*		1.79 (7.2)	-0.02*	-2.03^	
C8	Standing open water and canals				0.07*	-3.81$^{\$}$		0.11^		-0.56 (0.4)
C1:C5									-17.76*	
C2:C5								-0.003*		
C2:C4	Two-way interactions		4.55*							
C2:C3						10.13*				
C3:C5					0.002*					
C3:C6		0.01*								
C0	Constant	-1.42*	-0.97*			-1.96*			0.07	

* < 0.001; $^{+}$ < 0.01; ^ < 0.02; $^{\$}$< 0.05

2.5. Discussion

The abundance models performed well in describing the species-environment relationship of deer in Great Britain, and the performance of those models in predicting an independent data set of species' observed distributions was comparable to the performance of models using presence/pseudo-absence or presence-only data (Table 2-1). The abundance models predicted areas of suitable habitat beyond the observed ranges of muntjac and red deer, highlighting the potential for range expansions in the future, given sufficient opportunities to spread. I consider these results in light of the habitat preferences of the focal species, the implications for their potential spread, and the utility of abundance data for modelling the distributions of species that are not in equilibrium with their environment.

The habitat preferences identified in the abundance models (Table 2-2) largely conform to the known preferences of the three species (Chapman et al. 1994, Harris et al. 1995), and are similar to the habitat predictors used in previous models of habitat suitability for the three focal species (Acevedo et al. 2010). I tested models using an independent dataset, rather than the data used to train the models, on the basis that 'validation is preferable to verification' (Araujo and Guisan 2006). Inevitably, therefore, the performance statistics (Table 2-1) were lower than those of previous studies which did not use an independent dataset for model validation (Acevedo et al. 2010). Once I had assessed model accuracy, I used the best models to predict habitat suitability beyond species' current ranges. To do this, I needed to convert model outputs into binary presence/absence predictions. There is currently debate regarding the subjectivity of choosing a threshold to convert predictions into presence/absence predictions (see, for example, Liu et al. 2005, Freeman and Moisen 2008). Many different thresholds are used, ranging from an arbitrary threshold of 0.5 (e.g. Manel et al. 1999, Acevedo et al. 2010), a threshold which maximises Cohen's kappa (e.g. Araujo et al. 2006, Elith et al. 2006, Thuiller et al. 2006b, Hole et al. 2009), a threshold which minimises falsely predicted absences (Gormley et al. 2011), and a threshold which maximises sensitivity (correctly predicted presences) and specificity (correctly predicted absences) (e.g. Brotons et al. 2004, Thuiller et al. 2006a, Thuiller et al. 2006b, Franklin et al. 2013). In this particular case, the abundance models were expected to predict areas of suitable habitat outside of the baseline range, which

would technically be termed a false absence; under this scenario, if a threshold was chosen to maximise specificity the abundance models would be penalised relatively more than the presence only or presence/absence predictions. As such, a threshold was chosen which maximised the True Skill Statistic (TSS) (Allouche et al. 2006). This strikes a balance between maximising sensitivity and specificity, and has been used by others predicting the spread of invasive species (Gasso et al. 2012).

By fitting abundance models only to sites within the current range of each species and by excluding spatial variables from the models, I was able to extrapolate the models beyond the observed (current) range of a species to identify locations that species may (re)colonise in the future. For example, much of Wales was predicted to be highly suitable for red deer, despite their absence from most of these areas at present (Figure 2-2). Red deer populations in Wales are currently extremely restricted, usually originating from escapees from deer parks, and even then only usually persisting for short periods before being culled (Carne 2000). The abundance models performed poorly in predicting the presence of red deer in some areas within their observed ranges, such as in East Anglia and the south-west of England (Figure 2-2). Low predicted suitability for red deer in these areas may be a combined effect of: (a) artificially low abundances in the lowlands of England due to culling and historical eradication, and (b) sites in the highlands being managed for high deer densities – driving the model-fitting process.

Muntjac, red and roe deer have been increasing in range and abundance in Britain in recent decades, with compound annual growth rates of 12%, 7% and 5% between the years 2003 and 2007, respectively (Ward et al. 2008). Notwithstanding other potential limitations to spread, I show that, in particular, muntjac and red deer (abundance models; Table 2-1) have the potential to colonise Britain much more widely in the future. Roe deer are already very widespread across Britain. That I under-predicted the range extent of this species (using all three modelling approaches; Table 2-2), highlights the possibility that roe deer may have recently started to occupy what was previously thought of as less favourable habitat. In the absence of management, the potential range expansion of red and muntjac deer into areas identified as suitable could have important implications for community composition and dynamics in those newly colonised areas, given the observed impacts of deer on other components of

biodiversity, including vegetation, invertebrates, small mammals and birds (Putman and Moore 1998, Ward 2005).

The abundance-modelling approach I present here could be applied to projections of future land cover to predict future habitat suitability across Britain. Such habitat suitability predictions (assuming either static or altered land-cover) could be incorporated into dynamic models (Keith et al. 2008, Anderson et al. 2009, Willis et al. 2009, Zurell et al. 2009, Franklin 2010, Huntley et al. 2010) without fear of inherent biases associated with modelling current habitat preferences using presence-absence data. While the abundance models can be used to infer which locations a species may spread to in the future, dynamic models can be used to inform when and how species may alter their patterns of distribution. Such dynamic models could be used to guide the future management of species; by determining areas where suitable habitat is present, and that a species may spread to, we have an opportunity to recommend management in advance of, or during, the early stages of (re)colonisation.

In general, the abundance-modelling approach (as with presence-only and presence/absence models) will have limited applicability where novel environmental types are found beyond the observed range of a species (Broennimann et al. 2007, Fitzpatrick et al. 2007, Medley 2009). However, for the study species and region used here, this was not an issue (as novel habitats were not found outside of present-day ranges and the abundance models were shown to predict habitat suitability on independent data well). That the abundance models were comparable in terms of AUC performance to both the presence/absence and presence-only models (Table 2-1), indicates that, where abundance data are available, it is advantageous to use these data in an appropriate modelling framework. Additionally, abundance data are often more readily available than assumed, given that presence/absence data are often derived from surveys which record the density or relative abundance of a species (Pearce and Boyce 2006).

Given that many species are now altering their ranges under environmental change (Root et al. 2003, Parmesan 2006), the assumption of presence-absence data accurately reflecting environmental preferences is becoming increasingly questionable. In light of this, when producing distribution models for species with expanding ranges,

I advocate the use of models which utilise abundance data from within the current or historic range of a species, where high abundances can be assumed to reflect a true preference for the habitat in that area (and *vice versa*). In this way, robust predictions of environmental suitability beyond observed ranges can be obtained.

Chapter 3 : Developing a spatially explicit population model to predict the spread of deer in Britain.

3.1. Abstract

Background: The use of mechanistic models has been advocated as a next-step in improving predictions of species distributions. However, such models are relatively underused, and have not been used to predict or quantify the pattern or rate of spread of deer at large spatial and temporal scales. Here, I aim to demonstrate that mechanistic models can be used to accurately simulate the present-day distribution of deer in Britain, and to quantify the influence of key demographic variables on their spread.

Methodology: A spatially-explicit population model was developed, and then tested by retrodicting the spread of roe *Capreolus capreolus*, muntjac *Muntiacus reevesi* and red deer *Cervus elaphus* in Britain between 1972 and 2007. Sensitivity analyses were carried out by re-running the models using a range of plausible parameter values representing survival rates and probability of breeding. Model performance was assessed by comparing observed to predicted distributions.

Findings: The model performed well in describing the pattern and rate of spread of roe (AUC = 0.70), red (AUC = 0.72) and muntjac (AUC = 0.79) deer between 1972 and 2007. For all three species, increasing survival rates significantly increased their spread, and accounted for a high proportion of variation in model performance (pseudo-R^2 between 0.23 and 0.72). Conversely, varying the probability of breeding had little or no influence on their spread, and accounted for a small proportion of variation in model performance (pseudo-R^2 between 0.00 and 0.20).

Conclusions: My results indicate that stakeholders can either facilitate or contain the spread of deer by influencing survival rates – altering fecundity was predicted to have little effect on the spread of deer. As the model accurately simulated the present-day distribution of deer in Britain, we can have confidence in using it to predict the potential future distribution of deer.

3.2. Introduction

Static, correlative modelling approaches – which relate species' observed distributions to environmental conditions – are often used to predict the potential future distributions of species (Beerling et al. 1995, Araujo and Guisan 2006, Thuiller et al. 2006a). While correlative approaches have proved important in highlighting the magnitude of expected changes in species distributions, estimates of potential future distributions generated using this approach are often overly-optimistic (Huntley et al. 2010). This is because many factors other than environmental suitability – such as dispersal ability, habitat connectivity and reproductive rates – influence range changes of species (Araujo and Guisan 2006). Consequently, the use of mechanistic models, which incorporate range-limiting processes, have been advocated as a next-step in improving predictions of the potential future distribution of species (Keith et al. 2008, Kearney and Porter 2009, Willis et al. 2009, Huntley et al. 2010, Merow et al. 2011, Fordham et al. 2012, Fennell et al. 2013).

Relative to correlative models, a major disadvantage of mechanistic models is that they require large amounts of species-specific demographic data which are often difficult to obtain (Naujokaitis-Lewis et al. 2009), leading to problems parameterising models accurately. In particular, data associated with species' dispersal, such as dispersal distances, probability of dispersing, and dispersal-associated mortality, are difficult to collect (Ruckelshaus et al. 1997) and are, consequently, rarely reported in the literature. Therefore, to develop such models a compromise must often be made between limiting a model to use only those data that can be easily obtained, and incorporating as much detail as possible to reflect reality (Radeloff et al. 1999).

Spatially explicit population models (SEPMs), which couple together a population (or individual) based model with a spatially explicit map of heterogeneous environmental suitability (Dunning et al. 1995), have been used to model the spatial distribution and abundance of a variety of taxa, including mammals (Rushton et al. 1997, Wiegand et al. 2004a, Bar-David et al. 2005, Marucco and McIntire 2010, Iordan et al. 2012), butterflies (Willis et al. 2009), beetles (Rushton et al. 1996), birds (Pulliam et al. 1992), squirrels (Rushton et al. 1997), and plants (Collingham et al. 1996). In addition to predicting the distribution of species, SEPMs can also be used to investigate how

variation in parameters, such as fecundity and rates of dispersal and survival, affect species distributions and population viability (McCarthy et al. 1995, Rushton et al. 1997, Keith et al. 2008). This is especially important as information on species-specific parameters such as survival- or pregnancy rates are often based on a few individuals or populations, or are simply unavailable (Dunning et al. 1995). Sensitivity analyses that vary parameter values from multiple model simulations can highlight the importance of traits in facilitating spread. Usually, individual parameters are altered in turn, to quantify the influence of that parameter on the model results (Dunning et al. 1995). Accordingly, sensitivity analyses can be used to assess the overall reliability of model predictions, identify parameters that have the greatest influence on model performance, prioritise data collection, and help to guide effective management strategies (Naujokaitis-Lewis et al. 2009).

Static, correlative modelling approaches have been used to describe environmental suitability for deer (e.g. Chapman et al. 1994, Pompilio and Meriggi 2001, Irvine et al. 2009, Acevedo et al. 2010; Chapter 2), and population models have been created for the purposes of deer management (e.g. Radeloff et al. 1999, Jennings 2009) and predicting the dynamics of deer re-introductions (Bar-David et al. 2005). However, these population models were either not spatially explicit (e.g. Radeloff et al. 1999), did not incorporate pertinent life-history parameters such as dispersal (e.g. Radeloff et al. 1999, Jennings 2009), or did not take into account the two major causes of non-natural mortality of deer: hunting and deer-vehicle collisions (DVCs). An estimated 500,000 DVCs occur each year in Europe (Bruinderink and Hazebroek 1996), with 74,000 in Britain alone (The Deer Initiative 2007), and approximately 350,000 adult deer are culled per year in the U.K. (Deer Initiative, in P.O.S.T. 2009).

Despite the intensity with which deer have been studied, only two research groups have incorporated deer demographics into a SEPM (Bar-David et al. 2005, Angold et al. 2006). The latter study created a SEPM to examine the effects of habitat fragmentation and connectivity on the viability of muntjac deer populations in Birmingham, U.K. Their model incorporated a habitat map with associated habitat suitability values, as well as undefined life-history information (undefined in their paper) for each species. Their SEPM was used to analyse population viability in the focal landscape; the authors found that the SEPM for deer was most sensitive to juvenile mortality, and that

muntjac deer were able to spread easily between fragmented habitat patches. However, the authors did not use their model to predict the spatial distribution of deer. Conversely, Bar-David *et al.* (2005) incorporated data on the release of 53 Persian fallow deer *Dama mesopotamica* into a SEPM to predict the spatial dynamics of their release. However, this study was limited due to its small spatial (165km^2) and temporal scales (5 years). Thus, until now, SEPMs have not been used to predict deer distributions or to quantify the pattern and rate of their spread across large temporal and spatial scales, and only one study (Angold et al. 2006) has investigated key processes influencing the spread of British deer, though on a regional scale and in an urban landscape.

Many SEPMs assume dispersing individuals show no directional choice (e.g. Collingham et al. 1996, Travis et al. 2011), or that individuals will move through a landscape across habitats with the highest quality, irrespective of whether those habitats are at carrying capacity (e.g. Willis et al. 2009). I aim to improve the biological realism of the dispersal process by:

- choosing dispersal direction in relation to both current occupancy and habitat suitability. The methodology I use is similar to a model developed to predict Iberian lynx *Lynx pardinus* movement (Revilla and Wiegand 2008); the dispersing individual is deemed to be aware of the habitat quality within their 'perceptual range' (defined as their eight neighbouring cells), and the choice of dispersal direction is dependent on habitat quality and occupancy within that range;
- accounting for the complex dispersal strategy of deer. Previous attempts to model dispersal in SEPMs have assumed that dispersal ends as soon as an individual reaches an unoccupied suitable cell (e.g. Pulliam et al. 1992). Instead, the SEPM described here incorporates a 'stopping rule', whereby dispersal is modelled as a discrete number of steps and during each step a probability of continued dispersal is applied: if this value is high, many individuals continue to disperse until the maximum number of steps, and if this value is low, the individuals typically stop dispersing as soon as cell where number of resident individuals is lower than the carrying capacity is reached;

- and treating the edge of the modelling arena (i.e. the British coast) as a 'reflective boundary'. So, rather than leaving the modelling arena (e.g. Collingham et al. 1996), an individual will change dispersal direction instead (following Pulliam et al. 1992).

This chapter is split into two sections. In the first section, I describe the development of a SEPM to predict the spread of deer across a heterogeneous landscape. In the second section, I validate the model by combining the outputs of habitat suitability models (developed in Chapter 2) with species-specific demographic parameters obtained from the literature to retrodict the spread of roe, red and muntjac deer in Britain between 1972 and 2007. Model performance is assessed by seeding models with distributions from 1972, modelling population spread to 2007, and comparing observed and predicted distributions in 2007. I then conduct sensitivity analyses to assess the influence of pregnancy and survival rates on the spread of deer, and therefore model performance. Finally, I incorporate deer-vehicle collisions into the SEPM, and assess the effect of this addition on model performance.

3.3. Methods

3.3.1. Structure of the Model

The SEPM simulates the spread of an organism across a heterogeneous landscape. It is a grid-based model, with each cell in the landscape representing 1km^2; this resolution was chosen as the majority of dispersing deer move only a few kilometres from their natal ranges (see, for example, Chapman et al. 1994, Staines et al. 1998, Radeloff et al. 1999, Daniels and McClean 2003), and so the model needed to operate at this small spatial scale (following Radeloff et al. 1999, Angold et al. 2006). At the start of the modelling procedure, the grid is populated with the initial distribution of the organism of interest and a habitat-suitability value is assigned to each cell in the modelling arena. Subsequently, for each time step and for each cell across the landscape (in a random order), the number of individuals surviving, breeding and dispersing are calculated. The SEPM models females only, as they "predominantly dictate the population dynamics of ungulates" (Bar-David et al. 2005). Pseudo-code describing the timing of different processes that occur in the model is shown in Figure 3-1, and the parameters and input data required by the model are described in the next few pages.

The carrying capacity for a species in each cell is linearly proportional to the habitat suitability in that cell. If the number of individuals in a cell at any point exceeds the carrying capacity the excess are forced to disperse or they die. In addition, individuals below the carrying capacity may also disperse, according to a set probability. The maximum number of dispersal steps an individual can take each time step (equivalent to the inter-birth interval of that species) is provided by the user.

3.3.2. Model parameters

The SEPM requires a number of parameters (summarised in Table 3-1). As I am modelling females only, maximum carrying capacities and number of offspring are adjusted according to adult sex ratio and birth sex ratio, respectively. For example, for a species that produces twins and whose sex ratio at birth is 1:1 (males:females), the number of offspring produced is reduced by half. For a species with a 1:2 adult sex ratio, maximum carrying capacity values are reduced by a third to remove males from the model. The carrying capacity of each cell (equation 3-a) is calculated by rounding, to the nearest integer, the product of the adjusted maximum carrying capacity value and habitat suitability, *S*:

$$\boldsymbol{K = \lfloor MaxK * S \rceil} \qquad \textit{Equation 3-a}$$

Any individuals above the carrying capacity in a cell are forced to disperse: this is termed saturation dispersal. However, a number of individuals below the carrying capacity also disperse (termed pre-saturation dispersal), according to a set probability (*pOptDisp)*. For example, if this value is set to 1, all individuals in the cell will disperse even if the cell is below carrying capacity. For each dispersal step during each time period, *pOptDisp* is applied to each dispersing individual to determine whether it carries on dispersing; at its extreme values, if *pOptDisp* is set to one, dispersing individuals will remain as dispersers until the maximum number of dispersal steps (*DispersalSteps*), and the resultant dispersal kernel has a fat tail. Conversely, if *pOptDisp* is set to zero, dispersing individuals will become resident in the first cell they disperse to where number of residents is less than carrying capacity, and the dispersal kernel has a thin tail. All probabilistic processes (Table 3-1) are determined as the outcome of Bernoulli trials. As such, a random number between 0 and 1 is generated preceding each probabilistic process throughout the modelling procedure; if that

number is greater than or equal to the probability of, for example, breeding, surviving or dispersing, that event occurs, and *vice versa*.

Initialise starting population, and define habitat suitability.

For each time step:

For each cell:

If there are individuals in the cell, stochastically determine the number of breeders, and the number of offspring per individual;

Apply independent survival rates to adults and juveniles;

Calculate the number of dispersers in that cell i.e. those over carrying capacity plus some that undertake optional dispersal.

For each dispersal step (up to a chosen maximum value):

For each cell, chosen in a random order:

For each dispersing individual:

Find adjacent cell (or origin cell if this is not step 1) with the highest suitability (or choose randomly between more than one of equal value) and move there;

Apply cost of dispersal in terms of road mortality (if included as an option in the model);

Store the end destination as the next step's origin, or, if the maximum number of steps has been reached, store as the end destination for that individual.

Incorporate new arrivals into cell's population.

Apply hunting mortality rates to each individual in each cell;

Age juveniles into yearlings, yearlings into sub-adults and sub-adults into adults;

Remove the individuals in each cell above the carrying capacity;

Output the population size and spatial distribution of individuals in each age class.

Figure 3-1. Pseudo-code for a spatially explicit population model, used to simulate the spread of an organism across a heterogeneous landscape.

Table 3-1. A description of model parameters used in the spatially explicit population model.

Notation	Description
No.Generations	The number of time steps the model will run; each time step is analogous to inter-birth interval.
SurvA	Probability of adult survival
SurvJ	Probability of juvenile survival
pHuntingSurvival	Probability of surviving hunting
pBreedAdult	Probability of successful breeding for adults
pBreedJuvenile	Probability of successful breeding for juveniles
ageFirstBreed	Age at first breeding
MaxK	Maximum carrying capacity in a cell with perfect habitat suitability
DispersalSteps	Maximum number of dispersal steps (km)
pOptDisp	Probability of optional dispersal
S	Habitat suitability in each grid square
pSingleton	Probability of producing a single offspring
pTwin	Probability of producing twins
birthSexRatioSingleton	Birth sex ratio of singleton offspring
birthSexRatioTwin	Birth sex ratio of twin offspring
birthSexRatioTriplet	Birth sex ratio of triplet offspring (calculated as: 1- *birthSexRatioSingleton- birthSexRatioTwin*

3.3.3. Modelling life history processes

The SEPM explicitly incorporates a number of key life history processes, which are summarised below.

i. *Breeding*

The number of offspring per individual is calculated at the start of each time step. For each individual over the age at first breeding (*ageFirstBreed*), the focal individual breeds depending on the age-specific probabilities of breeding (*pBreedAdult* for adults or *pBreedJuvenile* for juveniles). The breeding individual produces twin, singleton or triplet offspring according to set probabilities (*pTwin, pSingleton* and [1-*pSingleton*-*pTwin*], respectively). The number of offspring is then adjusted according to the birth sex ratio, which may vary according to litter size (*birthSexRatioSingleton, birthSexRatioTwin, birthSexRatioTriplet*).

ii. Survival

Age-specific survival rates (*SurvA* and *SurvJ*) are applied to each individual at the start of each time step – survival is based on the outcome of Bernoulli trails, as described on page 45. Hunting mortality (*PHuntingSurvival*) is also applied each time step; how this parameter is calculated for deer is described in further detail on page 53.

iii. Dispersal

Dispersal of deer involves two processes. First, for each disperser, for each dispersal step, the destination cell is chosen according to habitat suitability, carrying capacity and the number of resident individuals. Second, once the destination cell has been identified, movement takes place and the number of individuals in the destination cell is updated.

Finding the disperser's destination

For each dispersing individual, the 'weight' of each of the nine possible destination cells is calculated by taking the habitat suitability, *S*, carrying capacity, *K*, and the number of individuals in each cell into account (Equation 3-b):

$$\boldsymbol{Weight = S * \left(1 - \frac{nd}{K}\right)} \qquad \textbf{Equation 3-b}$$

where nd is the number of residents in the focal cell, and *K* is the carrying capacity (from equation 3-a).

The destination cell is chosen from one of the eight cells adjacent to the focal cell, and is based upon each cell's weight; the larger the weight the more attractive a cell is. A schematic of the movement process is given in Figure 3-2, and is described below.

The focal individual will move to the cell with the highest weight. If there are two or more cells with equal highest weights, then the destination cell is chosen randomly between those cells. If the focal individual is on its first dispersal step, it is forced to move from its origin cell. However, in subsequent dispersal steps (if *DispersalSteps* is greater than 1), the focal individual can remain resident if the new origin cell is the most 'attractive' of the nine options.

Moving

Once the destination cell has been identified, movement takes place and the number of individuals in the destination cell is updated. If the number of individuals in the destination cell exceeds carrying capacity, then all of the individuals over the carrying capacity remain as dispersers until at least the next time step. A number of individuals below the carrying capacity also disperse, according to a set probability (*pOptDisp*).

3.3.4. Retrodicting the spread of deer between 1972 and 2007

Parameter estimates used in the baseline models for red, roe and muntjac deer are shown in Table 3-2. Each of the parameter estimates were taken from the literature (where available), and are described in detail in Appendix 2 (and on page 52 for '*numberofseedcells*').

Table 3-2. Parameter estimates used in models to predict the spread of roe deer, muntjac deer, and red deer in Britain. Each of the parameter estimates were obtained from the literature (see Appendix 2), with the exception of the 'number of seed cells' (see Input data for deer models, below).

		Baseline value (species)		
Parameter	Description	Roe	Muntjac	Red
SurvA	Probability of adult survival	0.95	0.86	0.95
SurvJ	Probability of juvenile survival	0.83	0.75	0.69
pHuntingSurvival	Probability of surviving culling	^	^	^
pBreedAdult	Probability of successful breeding (adults)	0.81	1.00	0.90
pBreedJuvenile	Probability of successful breeding (juveniles)	0.66	0.60	0.50
MaxK	Maximum carrying capacity (number of individuals)	19	35	27
DispersalSteps	Maximum number of dispersal steps (km)*	20	13	31
pOptDisp	Probability of optional dispersal	0.05	0.05	0.00
pSingleton	Probability of producing a single offspring	0.27	1.00	1.00
pTwin	Probability of producing twins	0.72	0.00	0.00
birthSexRatioSingleton	Birth sex ratio of singleton offspring	0.60	0.50	0.55
birthSexRatioTwin	Birth sex ratio of twin offspring	0.51	n/a	n/a
birthSexRatioTriplet	Birth sex ratio of triplet offspring	0.50	n/a	n/a
AgeFirstBreed	Age at first breeding	1	1	2
No.Generations	Number of time steps the model will run over	35	53	35
numberofSeedCells	Number of 1km^2 cells to seed population in (of 100 possible cells)	10	90	10

*this is the maximum recorded dispersal distance in km (see Appendix 2); ^these species-specific values vary spatially and temporally according to culling density per county (see page 55).

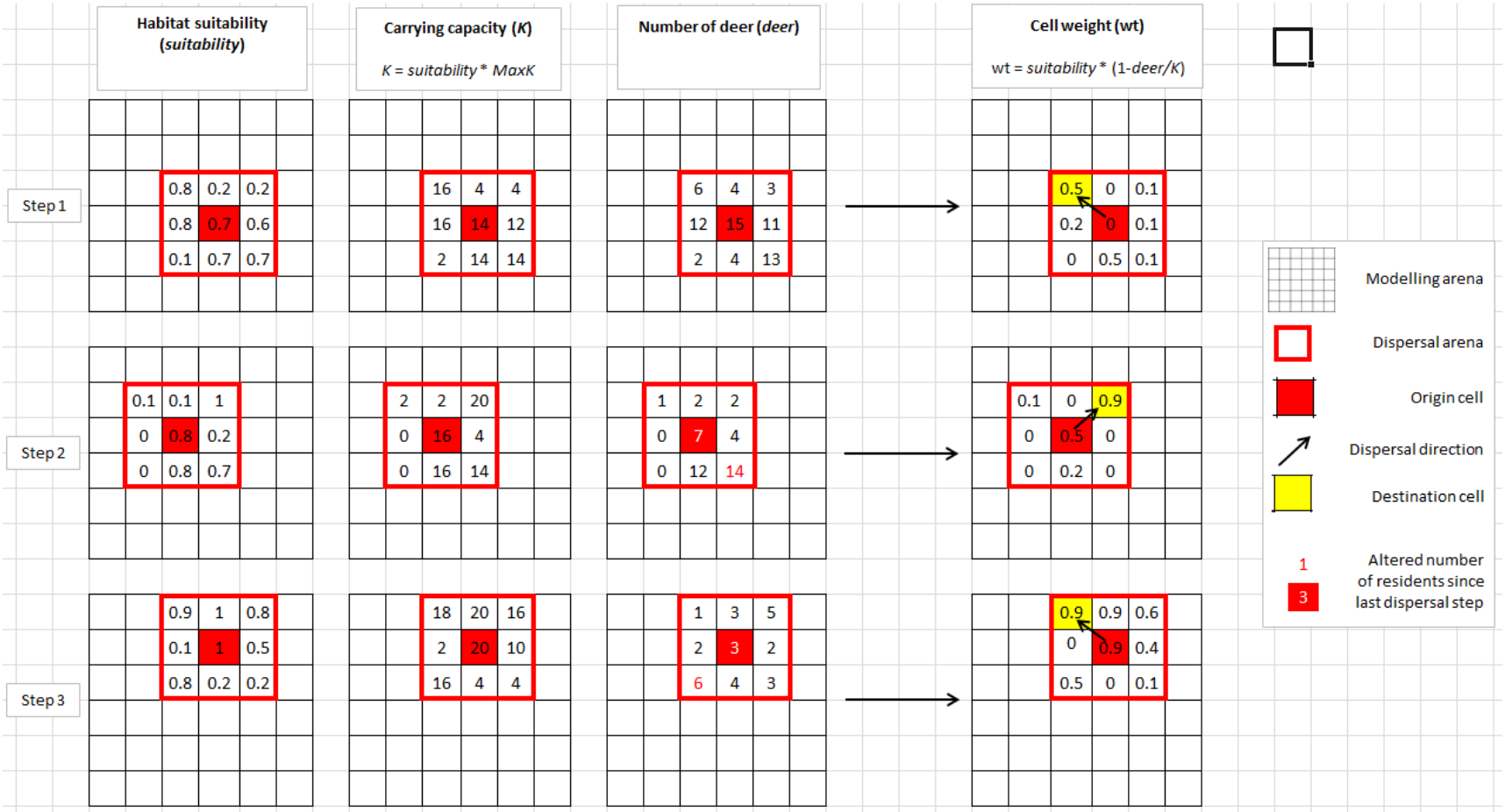


Figure 3-2. Schematic of dispersal rules over three dispersal steps. Cell weight is calculated using habitat suitability, carrying capacity and the number of resident individuals, as per the diagram. Dispersal direction is chosen as the cell with the highest weight – if two or more cells have the same highest weight, then dispersal direction is chosen randomly. The focal individual must move in the first dispersal step, but is then allowed to remain resident (depending on probability of dispersal, *pOptDisp*) in subsequent steps if the focal cell has the highest weight.

3.3.5. Input data for deer models

Habitat suitability (and associated carrying capacities) for deer in Britain

Modelled habitat suitability at a 1km^2 resolution across Britain was taken from the abundance models developed in Chapter 2 (Figure 3-3). Carrying capacity in each 1km^2 grid square across the U.K. was calculated using equation 3-a, using density estimates in prime habitats (***MaxK***), and adult sex ratios obtained from the literature (Appendix 2).

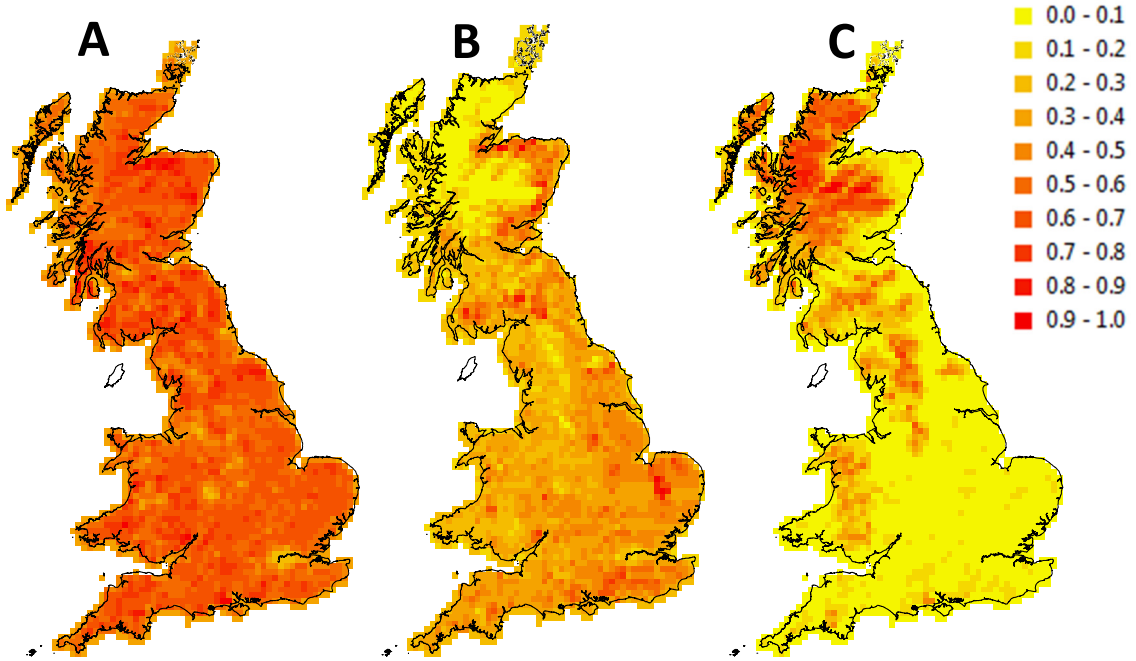


Figure 3-3. Habitat suitability for (A) roe deer, (B) muntjac deer and (C) red deer in Britain, obtained using abundance-models described in Chapter 2. Values fall between zero (low predicted habitat suitability) and one (high predicted habitat suitability).

Seed distributions of deer in Britain

Observed distributions of muntjac, roe and red deer in Britain at a 10km^2 resolution in 1972 and 2007 were downloaded from the National Biodiversity Network (NBN; available from: data.nbn.org.uk), and augmented by observations collected on an *ad hoc* basis by members of the British Deer Society (Figure 3-4). Models were seeded using the presence/absence data from 1972, following two steps. First, the optimal number of 1km^2 seed cells to use in the models for each species was calculated (see next paragraph). Second, each 1km^2 seed cell was filled to carrying capacity (equation 3-a).

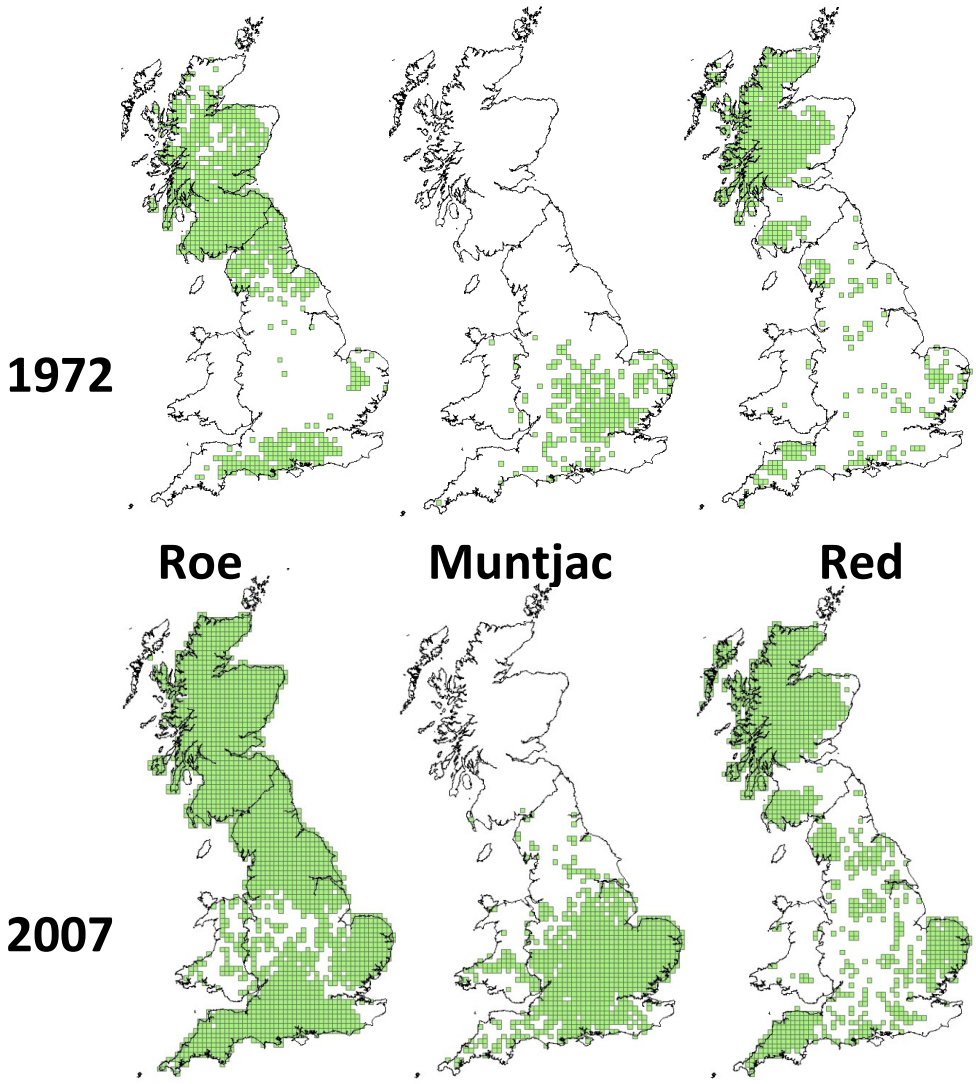


Figure 3-4. Observed distributions of roe deer, muntjac deer and red deer in Britain in 1972 and 2007, obtained from the British Deer Society and the National Biodiversity Network. Green squares represent species' presence in a 10km^2 cell.

Ten different sets of models were run for each species, with ***numberofSeedCells*** (number of 1km^2 grid squares) set as 10, 20, 30, 40, 50, 60, 70, 80, 90, or 100 (equating to each 10km^2 grid square being between 10 and 100% filled to capacity). All other parameters were kept constant (baseline parameters; Table 3-2). Each model was run 30 times, to account for stochasticity among model runs. The performance of each model in predicting the observed distribution of each respective species in 2007 was assessed by calculating AUC.

For all species, changing the number of seed cells caused a slight but perceptible alteration in the performance of the models (Figure 3-5). The number of seed cells

used in baseline models was therefore chosen as the number that yielded the highest median AUC (roe and red deer = 10 seed cells, muntjac = 90 seed cells [Figure 3-5]).

Accounting for hunting in the SEPM

I accounted for hunting mortality in the model using data on the density of shot deer in each county of the U.K., obtained from the National Gamebag Census (NGC) which is organised by the Game and Wildlife Conservation Trust (GWCT) (Aebischer et al. 2011). The distributions of deer shot in Britain in each county of the U.K. between: (1) 1970 and 1979, (2) 1980 and 1989, and (3) 1990 and 1999, are shown in Figure 3-6. At the end of each time step, hunting mortality is applied using these data in a five-stage process. For each cell, I first identified the density of deer culled per km^2 (i.e. per cell, as I am modelling at this resolution) from the maps shown in Figure 3-6. Second, I took the mid-point of each density category as the approximate number of deer hunted in that year in that cell, and adjusted this figure to represent females only; to do this, I used data on the sex ratio of shot deer, obtained from records of shot deer obtained from the Ministry of Defence (Table 3-3).

Table 3-3. Numbers of species- and sex-specific records of shot deer on Ministry of Defence estates across the U.K. between 2006 and 2010, inclusive. Data were provided by the Ministry of Defence.

Species	# records	Proportion (number) of females shot
Roe	5500	0.53 (2908)
Muntjac	995	0.43 (385)
Red	332	0.39 (143)

Third, I calculated the probability of hunting mortality in that cell by dividing the number of females hunted (from step two, above) by the carrying capacity of that cell (equation 3-a). The probability of hunting mortality was capped at a value of 1 (otherwise, if the number of females hunted was greater than the carrying capacity the probability of mortality was greater than one). Fourth, the probability of hunting survival (*PHuntingSurvival*) was calculated as 1 minus the probability of hunting mortality. Finally, this probability of hunting survival was applied to each individual in each cell, as the outcome of Bernoulli trials. As the NGC culling density maps only run to 1999 (Figure 3-6), I took the conservative approach of assuming that culling density after that period (i.e. to 2007) remained at the same levels as recorded between 1990 and 1999.

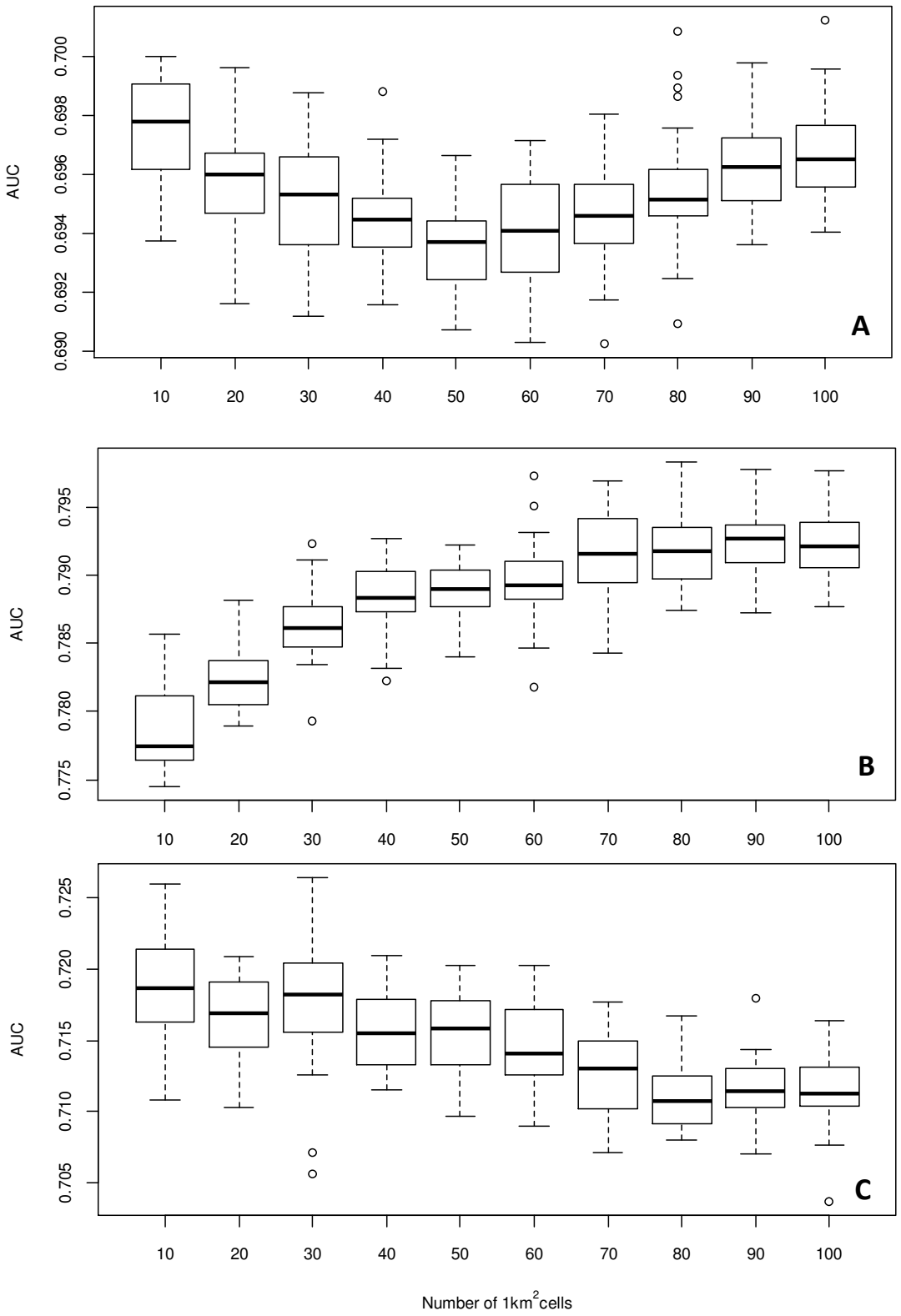


Figure 3-5. The performance of models with differing number of seed cells in predicting the distribution of (A) roe deer, (B) Chinese muntjac deer, and (C) red deer in Britain in 2007. Performance was assessed in terms of the area under a receiver operating characteristic curve (AUC). Models were run 30 times to account for stochasticity. The bold, black vertical lines represent median values across these 30 runs, upper and lower quartiles are defined by the end of the boxes, and maximum and minimum values by the whiskers. Outliers are represented by hollow circles. Note different y-axis scales.

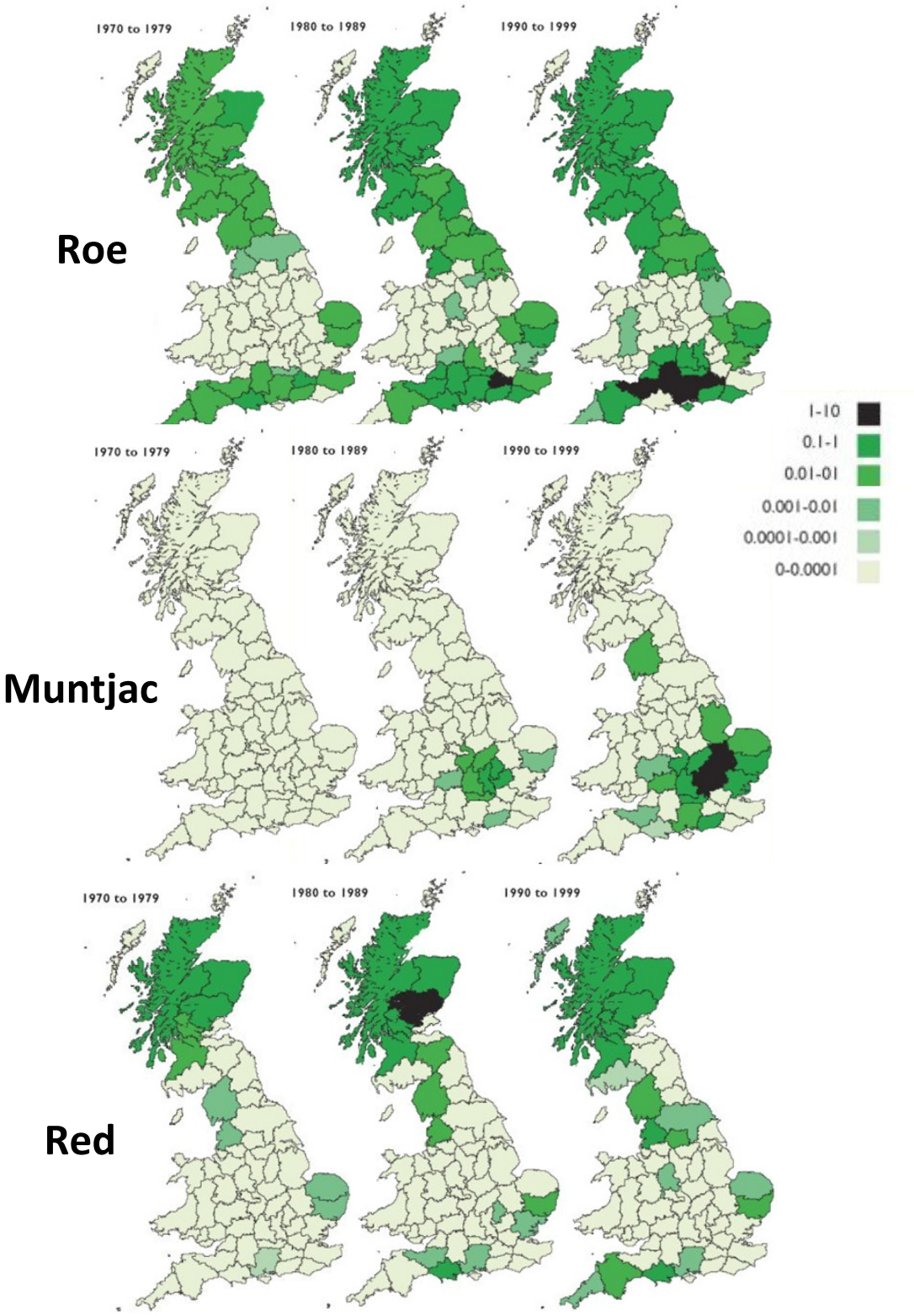


Figure 3-6. Changes in the distribution of shot roe, muntjac and red deer in Britain between 1970 and 1999. The scale represents the mean number of deer shot per 1km^2 in each county in Britain in each decade, with darker areas representing higher culling densities. These figures were taken from www.gwct.org.uk/research__surveys/wildlife_surveys_and_ngc/national_gamebag_census_ngc/mammals__comprehensive_trends_new/234.asp, accessed October 2013 (Aebischer et al. 2011).

3.3.6. Model validation: retrodicting the spread of deer between 1972 and 2007

Models were run for 35 generations for roe and red deer, and 53 generations for muntjac deer [as they can breed every 9 months (Chapman et al. 1997)], so that spread between 1972 and 2007 could be simulated. This allowed the performance of the models to be tested, by comparing the observed and predicted distribution of deer in 2007. Each model was run 30 times (using the baseline parameters described in Table 3-2), to account for stochasticity between model runs.

Observed and predicted distributions were compared following two steps. First, as models were run at a $1km^2$ resolution, and the observed data were at a $10km^2$ resolution, the predicted distributions from the model were upscaled to the resolution of the observed data (by summing the number of deer in each $10km^2$ cell). Second, model performance was assessed by comparing observed (Figure 3-4) and predicted occurrences in 2007. Performance was assessed after the exclusion of seed cells, so as to not artificially inflate the estimates of goodness-of-fit (following Willis et al. 2009). Overall accuracy of the model predictions was measured using the area under a receiver operating characteristic curve (AUC) (Allouche et al. 2006). Sensitivity (number of correct presences) and specificity (number of correct absences) of the model predictions was also calculated. Each measure of accuracy ranges from 0 to 1, with values of 1 being a perfect agreement. Sensitivity, specificity and AUC were calculated after exclusion of seed cells, to avoid inflating estimates of goodness-of-fit (following Willis et al. 2009). A further check of model performance was made by comparing the observed and predicted abundance of deer in 1995, as an estimate of roe, red and muntjac deer population size was made in that year (Harris *et al.* 1995 in Table 1-3).

3.3.7. Sensitivity of models to variability in survival rates and probability of breeding

Where parameter estimates from the literature were highly variable, models were run 500 times with parameter values chosen randomly between their observed upper and lower bounds (following Citta and Mills 1999). This enabled an evaluation of the relative importance of each vital rate on the spread of deer, and therefore model

performance. For roe and red deer, parameter estimates for adult and juvenile survival and the probability of adults and juveniles breeding were highly variable (Appendix 2). For muntjac deer, estimates of these parameters (with the exception of adult probability of breeding) were scarce (Appendix 2). The influence of each of these parameters on model performance was assessed following five steps.

First, upper and lower limits for each vital rate were obtained from the literature (Table 3-4; Appendix 2). For muntjac deer, parameter estimates for pregnancy and survival rates were chosen randomly between upper and lower bounds of observed values, as published data on these demographic rates were scarce; juvenile survival rate was varied between the same bounds as the similar-sized roe deer (Table 3-4), while upper and lower bounds of adult survival and probability of juvenile breeding were increased and decreased by 25%.

Table 3-4. Upper and lower bounds of parameter estimates used in models to predict the spread of roe deer, muntjac, and red deer in Britain. Descriptions of parameter descriptions are provided in Table 3-2, and further detail regarding references is provided in Appendix 2.

Species	Parameter	Min.	Max.	Reference(s)
Roe	*SurvA*	0.91	1.00	Cobben *et al.* 1999
	SurvJ	0.20	1.00	Gill 1994
	pBreedAdult	0.35	1.00	Hewison 1966
	pBreedJuvenile	0.67	0.94	Hewison 1966
Muntjac	*SurvA*	0.65^	1.00*	
	SurvJ	0.20*	1.00*	
	pBreedJuvenile	0.45^	0.75^	
Red	*SurvA*	0.80	1.00	Albon *et al.* 1987, Clutton-Brock *et al.* 2002
	SurvJ	0.45	1.00	Albon *et al.* 1987, Clutton-Brock *et al.* 2002
	pBreedAdult	0.60	1.00	Mayle 1996, Staines *et al.* 1998
	pBreedJuvenile	0.00	1.00	Mayle 1996, Staines *et al.* 1998

*chosen to be the same as the similar-sized roe deer. ^increased/decreased by 25% from the baseline value (Table 3-2).

Second, models were re-run 500 times for each species, with parameter values chosen randomly between their observed upper and lower bounds (Table 3-4), while all other parameters were kept at their baseline values (Table 3-2). Third, model performance (AUC, sensitivity and specificity) was assessed for each model replicate. Fourth, the relative importance of each parameter was assessed by regressing the model

performance metric against the randomly chosen parameter estimates used in the models. To do this, models with beta error distribution and a logit link [which allows for non-linear relationships between variables (Citta and Mills 1999)] were fitted using the 'betareg' package in R (as performance statistics [response variables] were bounded by 0 and 1; Cribari-Neto and Zeileis 2010, Simas et al. 2010). Finally, coefficients of determination (pseudo-R^2) (Nagelkerke 1991) were calculated for each model as a measure of how much variation in performance was explained by the variation in the parameter value.

3.3.8. Accounting for deer-vehicle collisions in models of spread

Previously, attempts to account for DVCs in a SEPM for deer did so by reducing the probability of survival of all individuals across the whole landscape by 0.06 (Jennings 2009). I built on this approach by accounting for the spatial distribution of DVCs in the SEPM, using the following methodology:

Data on number of DVC km^{-2} $year^{-1}$ and road length were obtained (see Table 1 in The Deer Initiative 2007). A generalised linear model was used to relate these two variables (Figure 3-7), and the modelled relationship was used to calculate the number of DVCs km^{-2} $year^{-1}$ across the whole of the British road network. To do this I used data on the length of individual roads, calculated from digitised maps of the road network. Then, for each $1km^2$ grid square, the total number of predicted DVCs per year on roads within that square was summed (to account for the fact that one grid square may include more than one road).

In Britain, the species of deer involved in DVCs is reported only in approximately 30% of cases (Langbein 2011). Of those, around 3% are estimated to involve red, sika and CWD, while the rest are split between fallow (40%), roe (32%) and muntjac deer (25%). There are approximately 74000 DVCs in Britain each year (Langbein 2011), and so I therefore estimated that 23680 DVCs would involve roe deer (i.e. 32% of 74000), 18500 would involve muntjac deer (i.e. 25% of 74000), and 740 (1% of 74000) would involve red deer each year. Data on temporal trends in the number and spatial distribution of DVCs are not available. Therefore, the estimated numbers of DVCs per species – described above – were used as a static measure of the numbers of DVCs per year in the SEPM.

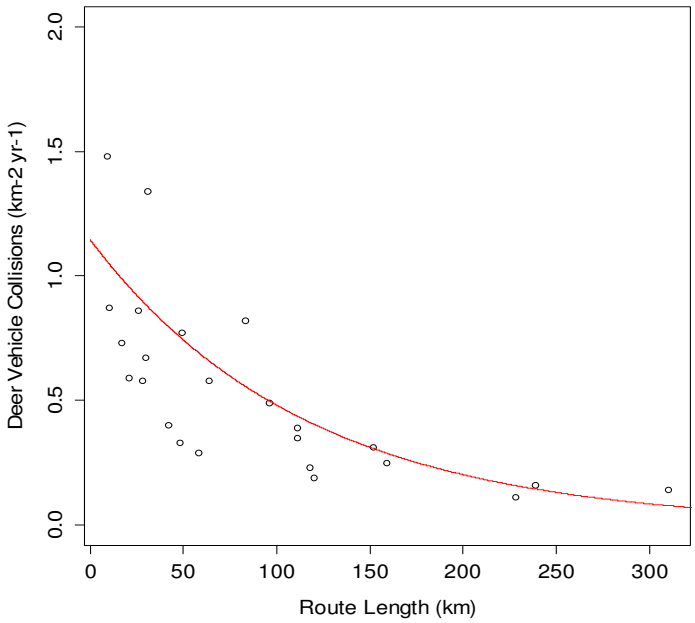


Figure 3-7. The negative, non-linear relationship between the length of a road and the number of deer-vehicle collisions (DVCs) per km per year. Hollow circles represent raw data obtained from a report written by the Deer Initiative (2007), and the red line shows the modelled relationship between road length and DVCs.

By multiplying the estimated number of DVCs in each grid square by the percentage of observed DVCs involving a given species (from the paragraph above), the predicted number of each species killed per year in each grid square was coarsely estimated. DVCs are accounted for as an additional, separate mortality event in the model (on top of the species- and age-specific survival estimates and hunting mortality applied to all individuals each year). At the end of each time step, the population in each cell is truncated according to the number of predicted DVCs in that cell.

As before, the SEPM, with baseline parameters for each species was seeded in 1972 and run to 2007, so that observed distributions and predicted distributions – with and without accounting for DVCs – could be compared. The mean number of predicted DVCs in each 10km^2 between 2003 and 2005 was calculated for each species, across each of the thirty model runs. The sum of predicted red, roe and muntjac deer DVCs in each grid square between 2003 and 2005 was then compared to the observed spatial distribution and abundance of DVCs (using observed DVCs in Britain between 2003 and 2005; The Deer Initiative 2007), as an additional test of model performance.

3.4. Results

3.4.1. Model validation: retrodicting the spread of deer between 1972 and 2007

The baseline models performed well in predicting the spread of roe, muntjac and red deer between 1972 and 2007, as demonstrated by the mean AUC values of 0.70, 0.79, and 0.72, respectively (Table 3-5). The SEPM did very well in predicting the extent of occurrence – measured by the number of predicted presences – of roe deer in 2007, but the baseline models for red and muntjac deer over-predicted their respective distributions (Table 3-5).

Table 3-5. Mean (± SD) sensitivity (correctly predicted presences), specificity (correctly predicted absences) and AUC of baseline models for roe, muntjac and red deer. Performance measures were calculated across 30 model runs, and after exclusion of seed cells in 1972. The numbers of observed and predicted (mean ± SD) presences (before exclusion of seed cells) in 2007, at a 10km^2 resolution, are also provided.

				No. of seed	No. of presences	
Species	AUC	Sensitivity	Specificity	cells	Observed	Predicted
Roe	0.70 (± 0.00)	0.76 (± 0.00)	0.64 (± 0.00)	915	2032	2037 (± 5)
Muntjac	0.79 (± 0.00)	0.71 (± 0.01)	0.87 (± 0.00)	246	824	941 (± 6)
Red	0.72 (± 0.00)	0.72 (± 0.01)	0.72 (± 0.00)	659	1211	1521 (± 5)

The models over-predicted the abundance of red, roe and muntjac deer in Britain in 1995 (Table 3-6). However, the predictions were within an order of magnitude of the observed abundances (which also represent males as well as females), which themselves are "accurate to within an order of magnitude" (Harris et al. 1995).

Table 3-6. Observed and predicted population size of muntjac, red and roe deer in Britain in 1995. Estimates of the observed population size of deer were taken from Harris *et al.* (1995), and predictions represent the mean (± SD) abundance of deer in Britain across 30 model runs, which were seeded in 1972 and run to 1995. Predictions represent females only; observed numbers include both males and females.

Species	Observed	Predicted
Roe	500,050	661,854 (**±** 1668)
Muntjac	40,300	71,799 (**±** 1048)
Red	359,550	359,563 (**±** 273)

The SEPM for muntjac deer predicted this species to be absent from counties where culling density was highest (compare Figure 3-8a and b). Therefore, from this point onwards, the maximum number of muntjac deer km^{-2} killed in locations where culling density was between 1 and 10 deer per km^2 (areas shaded in black in Figure 3-8b) was set to the lower end of the range, rather than the median value, as described previously.

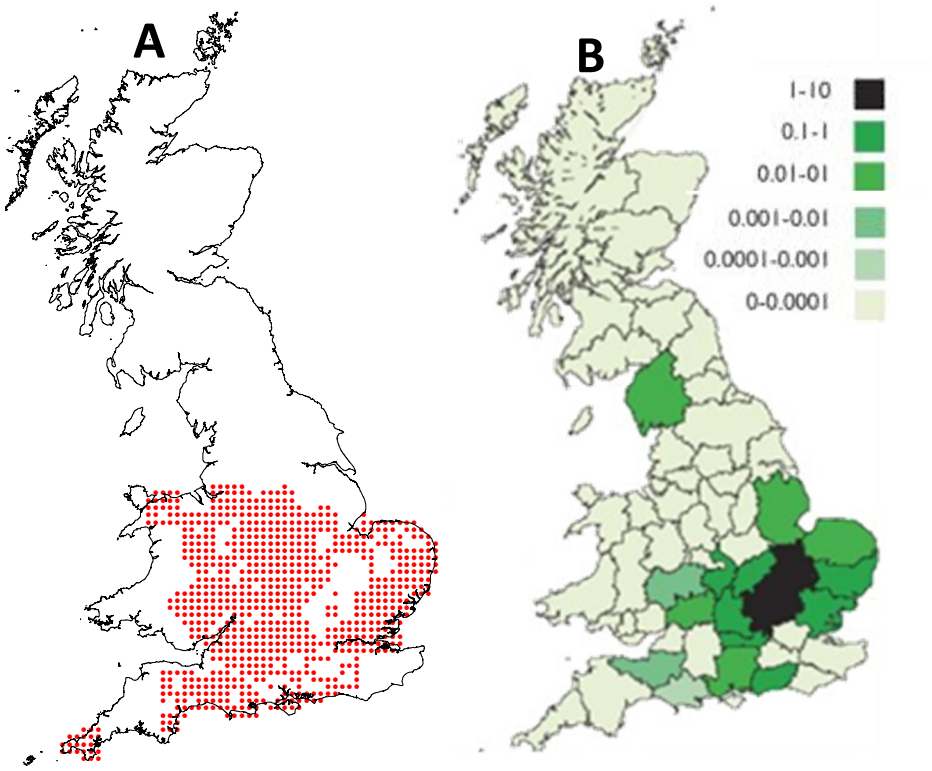


Figure 3-8. Predicted distribution of muntjac deer in Great Britain at a 10km resolution, represented by the red squares on map (A), showing predicted gaps in distribution in counties where culling density was highest (black areas in map B). The SEPM was seeded in locations where observed distribution data for 1972 were available (see Figure 3-9) and then run for 35 years to 2007, so that observed and predicted distributions could be compared. Map B shows the density of shot deer in British counties between 1990 and 1999 (see Figure 3-6 for more detail).

Resultantly, the SEPM predicted few locations where muntjac deer were present outside of locations where they were observed in 2007 (the exceptions being north Wales and southern Liverpool and parts of south-west England; Figure 3-9). Indeed, the spread of muntjac deer was under-represented by the models, particularly at the northern-eastern edge of their observed distribution, as well as in mid-Wales (Figure 3-9).

For the roe deer in particular, there was a circular pattern of expansion from the seed sites (Figure 3-9), which resulted from the relatively uniform, high habitat suitability values used in the model for this species (Figure 3-3). The models did well in predicting the observed, blanket distribution of roe deer across Scotland, eastern-, northern- and southern England by 2007. However, the observed presence of roe deer in Wales, around Peterborough, and in an east/west swathe from Cambridge to Gloucester was not well-predicted by the model (Figure 3-9).

The predicted distribution of red deer in 2007 matched the observed distribution well, especially in Scotland, eastern England, the Lake District and south-western England (Figure 3-9). Elsewhere, the observed distribution of red deer in 2007 was quite patchy, and, in general, the model either did not predict the presence of this species at all in those patches (for example, in the Brecon Beacons National Park in Wales), or over-predicted the distribution into locations surrounding those patches (for example, around Carmarthen, south-west Wales) (Figure 3-9).

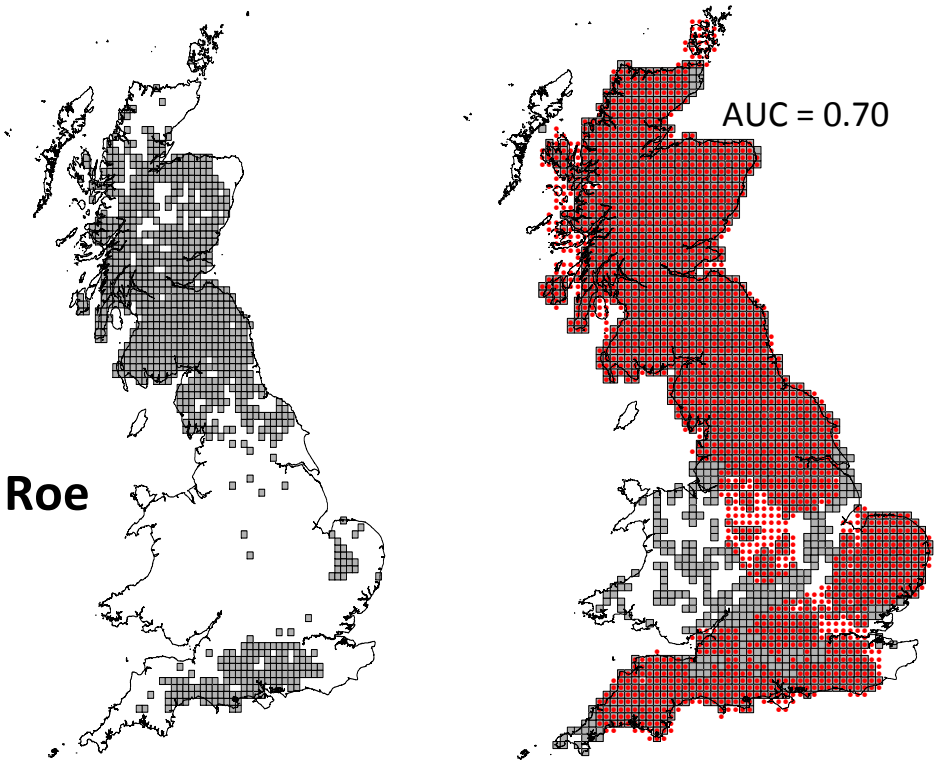


Figure 3-9. Observed and predicted distribution of roe deer, muntjac deer and red deer in Great Britain, at a 10km^2 resolution. Models were seeded in locations where observed distribution data for 1972 were available (grey squares on the left-hand-side maps), and then run for 35 years to 2007. Maps on the right-hand-side show observed (grey squares) and predicted (red circles) distributions in 2007, taken from the AUC best model (AUC provided above each map) across the 30 model runs for each species. Figure continued on the next page.

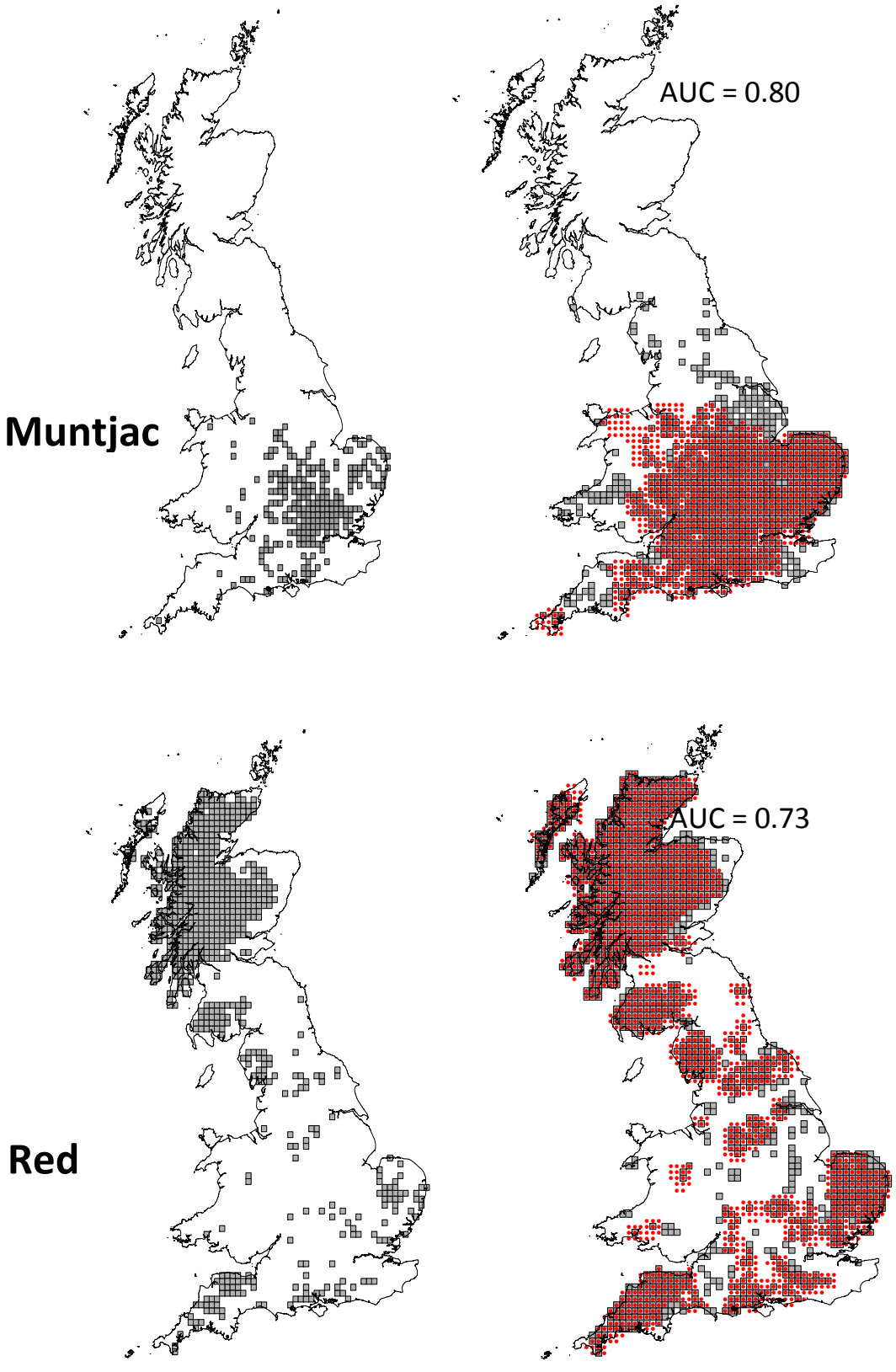


Figure 3-9 cont.

3.4.2. Accounting for hunting mortality

Approximately 350,000 deer are estimated to be culled per year, which represents by far the biggest cause of non-natural deaths of British deer per year (P.O.S.T. 2009). The predicted sums of deer killed in the model as a result of hunting are shown in Table 3-7. I estimated that approximately (to 3 *s.f.*) 63000 female roe deer, 16000 female red deer and 3150 female muntjac deer were culled per year between 2000 and 2007. Using the sex ratios of culled deer (Table 3-3), I was able to back-transform these values to obtain a rough approximation of the number of each species of both sexes predicted to be culled per year: 119000 roe deer, 40800 red deer and 7330 muntjac deer. Therefore, the model predicted that approximately 170000 roe, muntjac and red deer were culled per year between 2000 and 2007. A species-specific breakdown of the observed numbers of deer culled is not available.

Table 3-7. Predicted sums of female deer culled across the U.K. Values shown are the mean (± SD) numbers of each species killed across the 30 model runs, summed across each time period; values are broken down into groups corresponding to those used by the GWCT (see Figure 3-6).

	Number of deer killed due to hunting				
Species	1972 – 2007	1972 - 1979	1980 - 1989	1990 - 1999	2000 - 2007
Roe	45474 (± 24791)	11655 (± 2855)	43606 (± 2230)	66248 (± 10577)	63040 (± 865)
Muntjac	1985 (± 1605)	1 (± 0)	840 (± 37)	3785 (± 576)	3151 (± 33)
Red	11581 (± 5089)	4344 (± 1185)	12499 (± 1396)	14349 (± 599)	15915 (± 330)

3.4.3. Sensitivity of models to variability in survival rates and probability of breeding

Juvenile survival had a strong influence on spread of roe deer, accounting for a high proportion of variation in the performance of their models (pseudo-R^2 = 0.72; Figure 3-10). Conversely, adult survival had very little effect on the spread of roe deer, and therefore model performance (pseudo-R^2 = 0.03). However, it must be noted that the range of possible values for adult survival for this species was much more constrained than those of the other two species (Table 3-4).

For muntjac and red deer, both adult and juvenile survival had strong influences on their spread, accounting for between 50% and 23% of variation in model performance (Figure 3-11 and Figure 3-12). For all three species, there was a positive, non-linear

relationship between (juvenile and adult) survival and model performance (Table 3-8). In general, when juvenile survival rate was above approximately 0.8, and adult survival rate was above approximately 0.9, variation in model performance was minimised and model performance was maximised (Figure 3-10, Figure 3-11 and Figure 3-12).

Probability of juveniles breeding accounted for very little variation in the performance of the models for all species (Figure 3-10, Figure 3-11 and Figure 3-12). Probability of adults breeding accounted for 20% of the variation in roe deer model performance (Figure 3-10), but only 7% of variation in red deer model performance (Figure 3-12).

Table 3-8. Model selection results for roe, muntjac and red deer models relating model performance to probability of adult or juvenile survival (*SurvA* and *SurvJ*, respectively), or probability of adult or juvenile breeding (*pBreedA* and *pBreedJ*, respectively). The most parsimonious model (with the lowest AIC) for each parameter for each species is highlighted in bold.

			ΔAIC			
Species	Model type	*d.f.*	*pBreedA*	*pBreedJ*	*SurvA*	*SurvJ*
Roe	Linear	3	10.2	**0.0**	**0.0**	93.1
	Quadratic	4	**0.0**	1.8	0.6	**0.0**
	Piecewise linear	5	8.5	18.2	14.3	23.2
Muntjac	Linear	3	n/a	**0.0**	8.3	0.1
	Quadratic	4		2.0	**0.0**	**0.0**
	Piecewise linear	5		81.7	63.1	75.5
Red	Linear	3	0.3	**0.0**	38.8	17.0
	Quadratic	4	**0.0**	1.7	**0.0**	**0.0**
	Piecewise linear	5	40.8	51.0	44.5	48.0

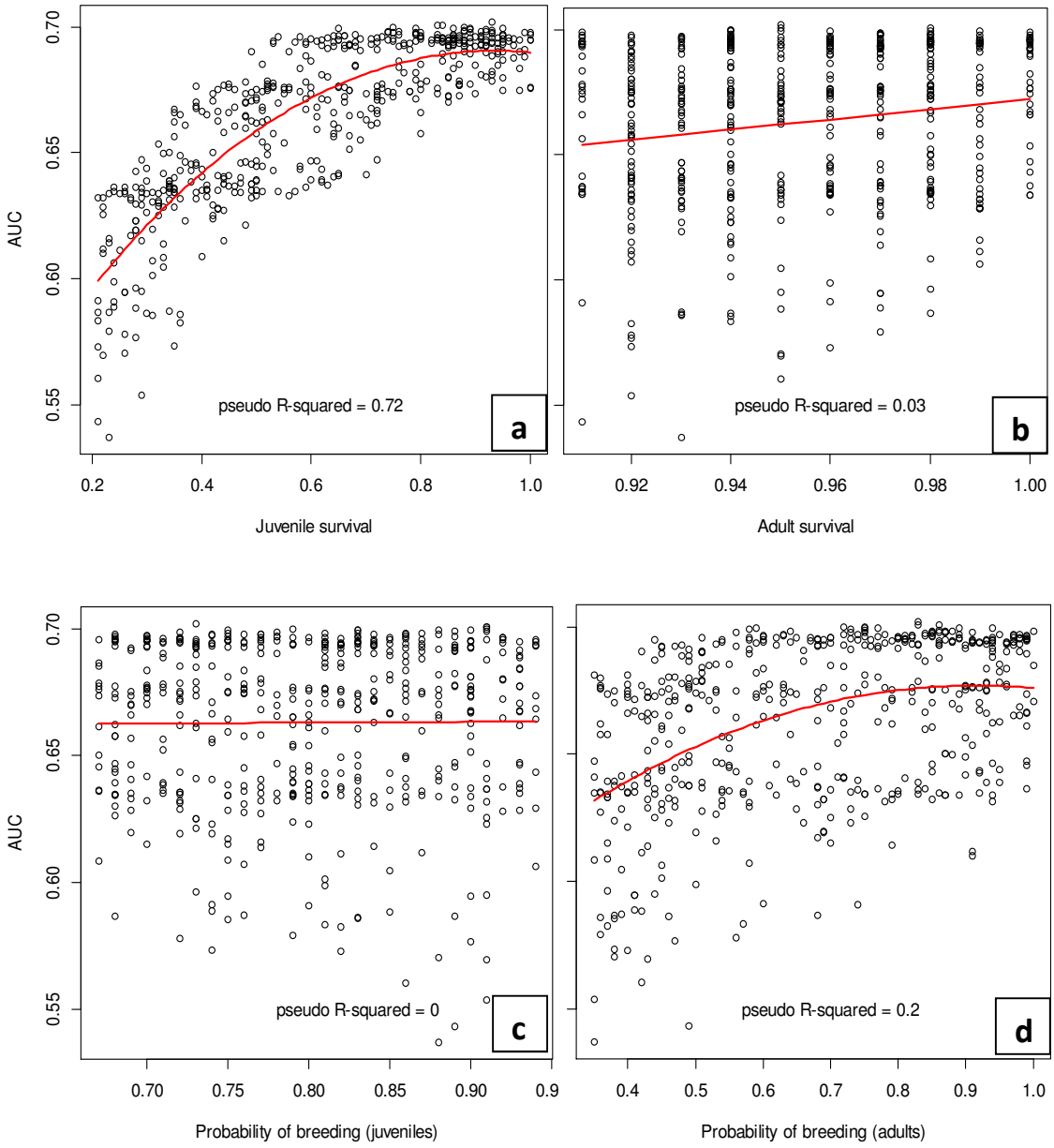


Figure 3-10. Amount of variation in roe deer model performances – assessed using AUC – accounted for by (a) juvenile survival rate, (b) adult survival rate, (c) probability of juveniles breeding, and (b) probability of adults breeding. Models were run 500 times, each with a randomly selected parameter value within the bounds of observed values (Table 3-4). Regression lines and coefficient of determination (pseudo-R^2) of AIC best models (linear, quadratic or piecewise linear [Table 3-8]) are shown.

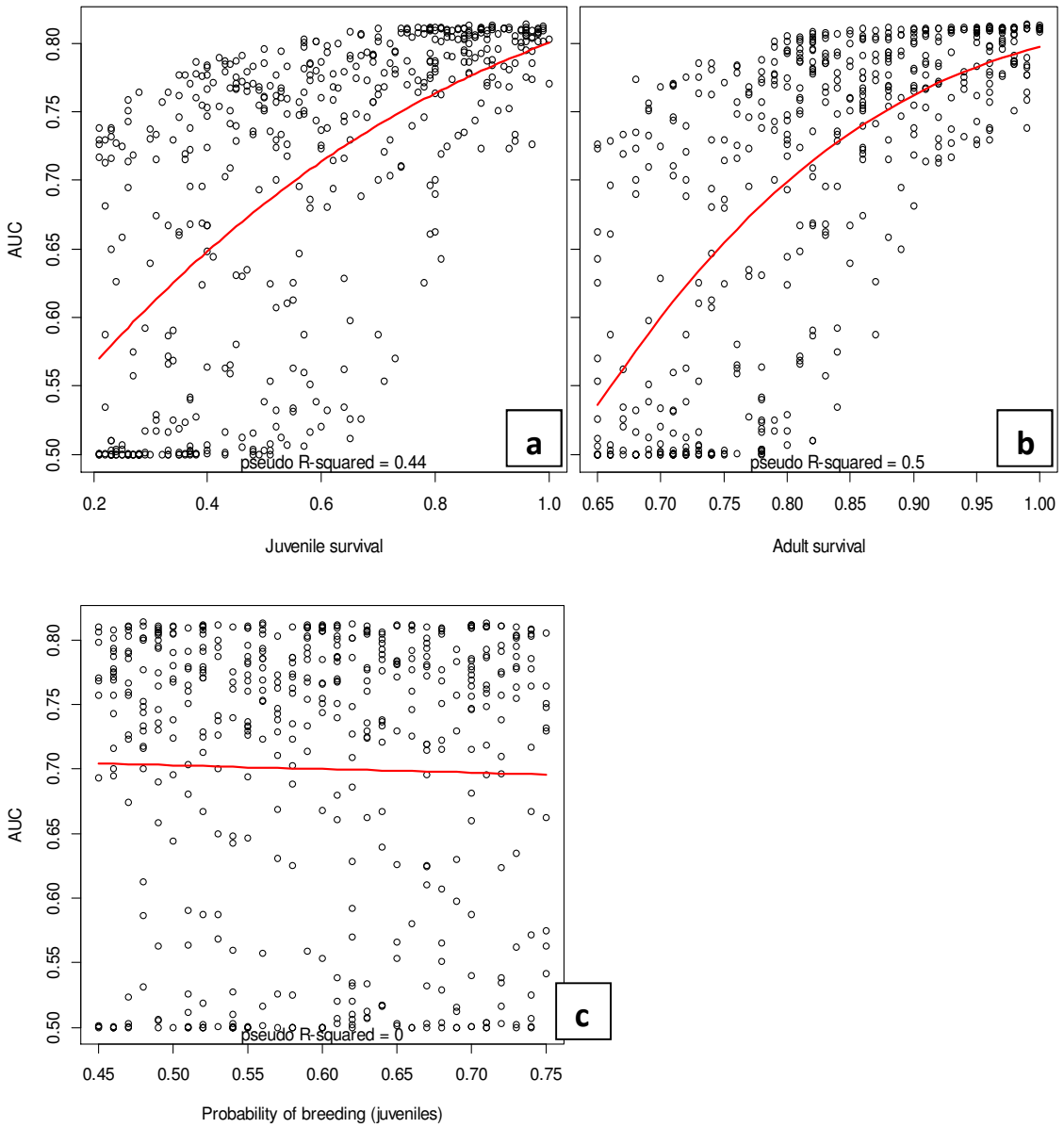


Figure 3-11. Amount of variation in muntjac deer model performance – assessed using AUC – accounted for by (a) juvenile survival rate, (b) adult survival rate, and (c) probability of juveniles breeding. Models were run 500 times, each with a randomly selected parameter value within the bounds of observed values (Table 3-4). Regression lines and coefficient of determination (pseudo-R^2) of AIC best models (linear, quadratic or piecewise linear [Table 3-8]) are shown.

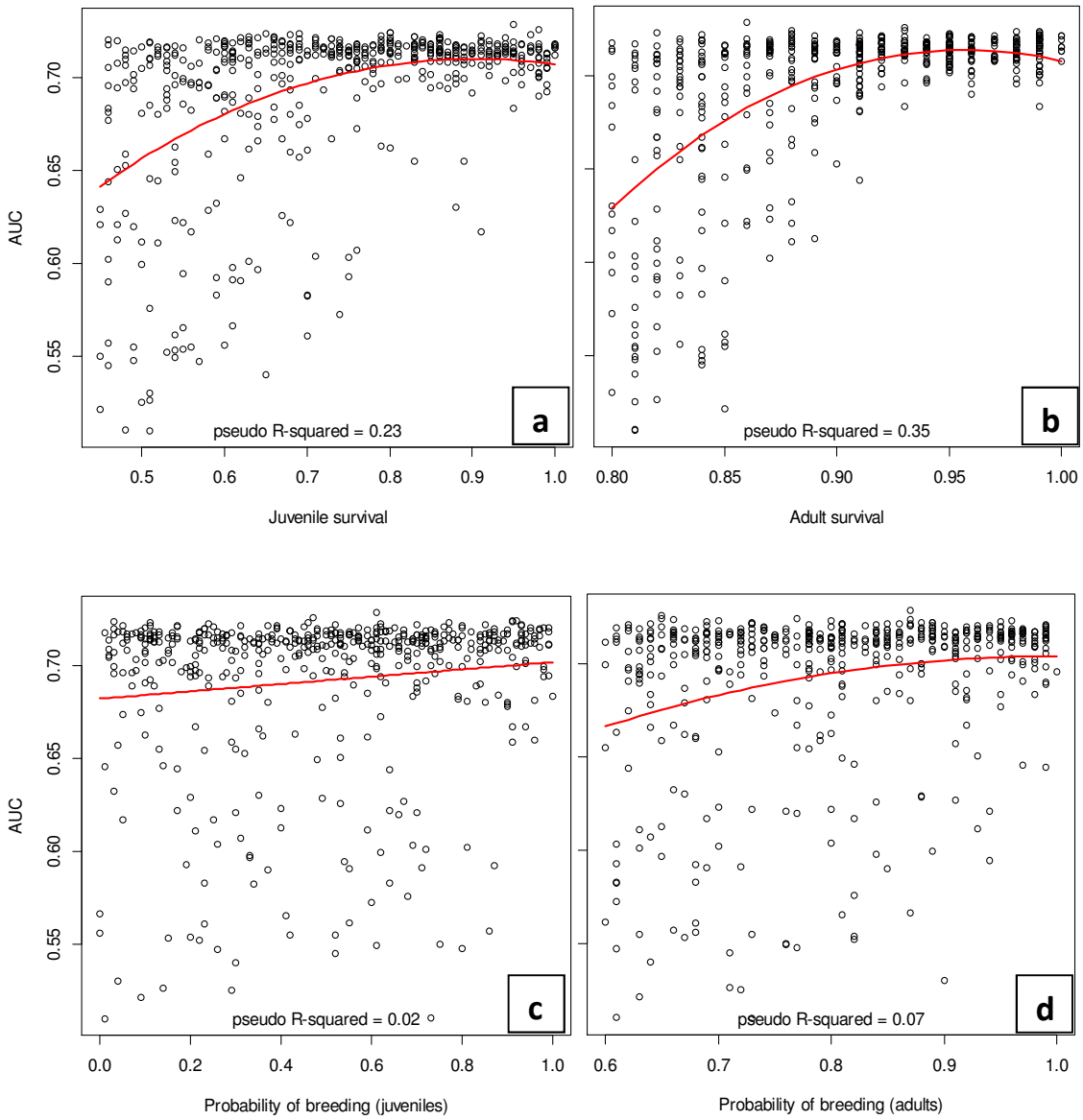


Figure 3-12. Amount of variation in red deer model performance – assessed using AUC – accounted for by (a) juvenile survival rate, (b) adult survival rate, (c) probability of juveniles breeding, and (b) probability of adults breeding. Models were run 500 times, each with a randomly selected parameter value within the bounds of observed values (Table 3-4). Regression lines and coefficient of determination (pseudo-R^2) of AIC best models (linear, quadratic or piecewise linear [Table 3-8] are shown.

3.4.4. Performance of the SEPM when accounting for deer-vehicle collisions

Accounting for DVCs significantly worsened the performance of the roe and muntjac deer baseline models (Mann-Whitney t-test roe deer $W = 204$, $p < 0.001$; muntjac deer $W = 0$, $p < 0.001$). Both of these results were a consequence of significantly slowing down the spread of deer when accounting for DVCs (Figure 3-13). For both species, there was a significant reduction in predicted presences when DVCs were included in the model (Table 3-9). Additionally, the SEPM including DVCs predicted gaps in muntjac deer distribution, again coinciding with areas of high culling density in Cambridgeshire (Figure 3-13), which points towards those areas having low predicted carrying capacity. No DVCs were predicted in any of the 30 replicate runs for red deer (see *Discussion*), and therefore there was no significant difference between the performance of baseline models and those which accounted for DVCs ($W = 427$, $p = 0.73$).

Table 3-9. Mean (± SD) sensitivity (correctly predicted presences), specificity (correctly predicted absences) and AUC of models predicting the distribution of roe, muntjac and red deer, calculated across 30 model runs, and after exclusion of seed cells in 1972. Performance of models not accounting for road mortality ('baseline'), and accounting for road mortality ('DVC') are provided. The number of observed and predicted (mean ± SD) presences (before exclusion of seed cells) is also provided.

					No. presences	
Species	Model	AUC	Sensitivity	Specificity	Observed	Predicted
Roe	Baseline	0.70 (± 0.00)	0.76 (± 0.00)	0.64 (± 0.00)	2032	2037 (± 5)
	DVC	0.69 (± 0.00)	0.70 (± 0.00)	0.70 (± 0.00)		1906 (± 5)
Muntjac	Baseline	0.79 (± 0.00)	0.71 (± 0.01)	0.87 (± 0.00)	824	914 (± 6)
	DVC	0.75 (± 0.00)	0.58 (± 0.01)	0.92 (± 0.00)		745 (± 6)
Red	Baseline	0.72 (± 0.00)	0.72 (± 0.01)	0.72 (± 0.00)	1211	1521 (± 5)
	DVC	0.72 (± 0.00)	0.72 (± 0.01)	0.72 (± 0.00)		1521 (± 8)

The models including DVCs predicted, on average (mean ± SD) 32121 ± 96 and 4103 ± 42 DVCs in 2007 involving roe and muntjac deer, respectively. This was a vast underestimate of the observed sum of DVCs involving muntjac deer, and an overestimate of the sum of roe deer DVCs (18500 and 23680, respectively; see page

59). However, it must be noted that the actual number of DVCs may be even higher than reported (Langbein 2011).

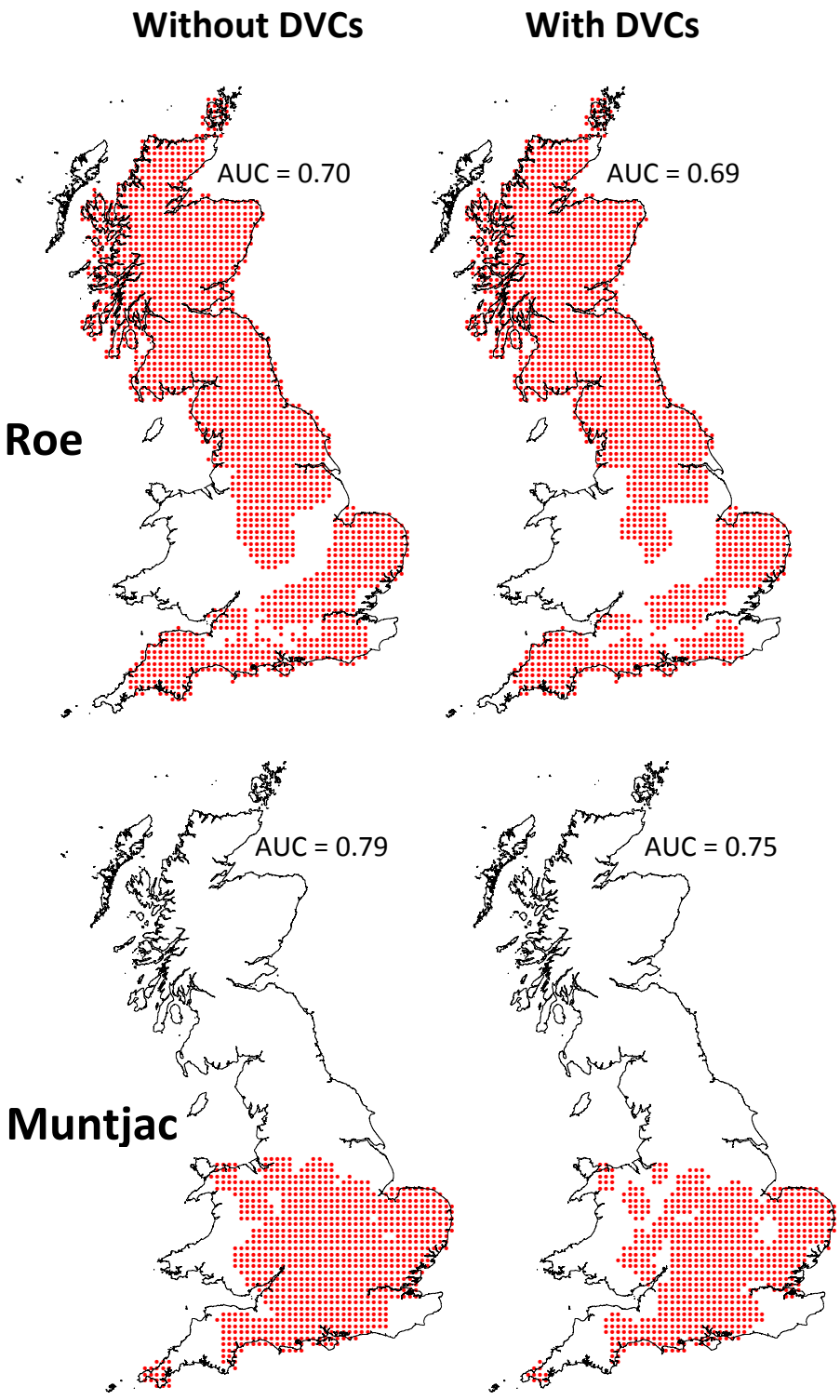


Figure 3-13. Predicted distribution of roe, muntjac and red deer in 2007, not accounting for deer-vehicle collisions (left), and accounting for DVCs (right). Models were run 30 times to account for stochasticity. For each species and each method, the predicted distribution from the model with the best AUC is shown.

The predicted pattern in number of DVCs involving roe and muntjac deer (there were no predicted red deer DVCs) between 2003 and 2005 showed hotspots around London, eastern- and north-eastern England, the midlands and the central belt of Scotland (Figure 3-14). These patterns matched the observed patterns of DVCs, with the exception of the midlands and north-eastern England, where the predicted number of DVCs were much higher than observed (Figure 3-14). Very few DVCs were predicted in Wales and the highlands of England and Scotland. The former because the models predicted very little spread in Wales (Figure 3-13), and the latter presumably because of the lower density of roads in the highlands.

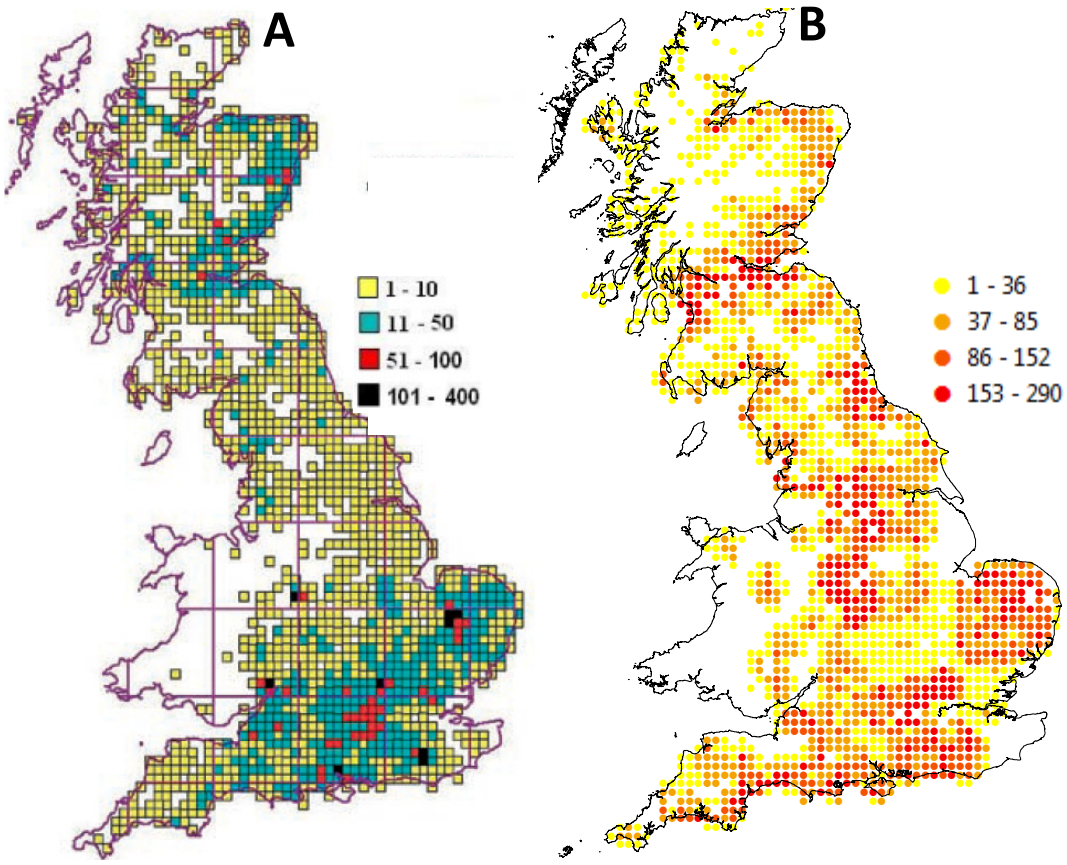


Figure 3-14. Observed (A) and predicted (B) number of deer-vehicle collisions in the UK between the years 2003 and 2005. The map of observed DVCs is taken from The Deer Initiative (2007), and shows number of reported DVCs involving all six species of British deer. The map of predicted DVCs shows the sum of the mean predicted DVCs in each 10km^2 grid square calculated across 30 model runs for roe, and muntjac deer. N.B. different scales and different number of species included in each map.

3.5. Discussion

Although SEPMs have been developed for other taxa (Pulliam et al. 1992, Collingham et al. 1996, Rushton et al. 1996, Rushton et al. 1997, Willis et al. 2009, Marucco and McIntire 2010), this is the first attempt to use a SEPM to predict deer distribution, and to investigate how changes in survival and probability of breeding may affect their spread at a national scale. The models did well in retrodicting the rate and pattern of spread of deer between 1972 and 2007 (Table 3-5; Figure 3-9). For roe deer in particular, there was a high agreement between the sums of 10km^2 cells observed and predicted to be occupied in 2007. The models for muntjac and red deer over-predicted the number of cells occupied by 2007 (Table 3-5). Despite this over-prediction, the muntjac deer models under recorded the patchy presence of muntjac in the north of their British range (Figure 3-9). These patchy observed distributions – between Darlington and Newcastle, and in Cumbria – are likely to be due to artificial translocations (Ward 2005), which were not accounted for in the model given the patchy and incomplete data regarding these events for this, and other species, in Britain (but see e.g. Whitehead 1964, Chapman et al. 1994).

It is likely that over-prediction by the SEPM is partly due to the under-recording of the observed distributions of deer (Ward 2005), which were used to validate the models. Under-recording of observed distributions was particularly noticeable in Wales (Ward 2005), which explains why the models performed poorly in predicting the observed distributions of roe deer in that country (Figure 3-9). The SEPM over-predicted the observed number of red, roe and muntjac deer in Britain in 1995 (Table 3-6), but were still within an order of magnitude of the observed abundances.

The maximum possible cull of muntjac deer was reduced in the SEPM as, using the original maximum cull density (Figure 3-6), total eradication of muntjac deer was predicted in counties such as Cambridgeshire and Hertfordshire (compare Figure 3-8 to Figure 3-9); this result is unrealistic given this species is observed to be present in those locations. The ‘incorrect’ predicted gaps in the distribution can be explained three ways. First, instead of being a linear relationship between carrying capacity and habitat suitability (as specified in the SEPM), the relationship may be non-linear. This would mean that carrying capacities may actually be higher than those used in the

SEPM in areas where culling density is observed to be high. Second, these predicted gaps in the distribution may result from inaccuracies with the habitat suitability layer – the predicted habitat suitability may in fact be higher in than the model predicts in those areas. Third, the categories of the levels of cull density from the GWCT (Figure 3-6) are crude; they are the same among all species (red, roe, muntjac, sika, fallow deer and CWD), and so the upper estimates in each category are likely to represent cull density of the large-bodied herding species rather than the smaller-bodied, less social muntjac deer.

The costs associated with the emigration from natal areas, and settlement into new areas is understudied (Bonte et al. 2012), and I was therefore unable to parameterise these costs in the SEPM at this stage. However, DVCs were incorporated into the SEPM given that data on the approximate number of DVCs is available for Britain (The Deer Initiative 2007). Accounting for DVCs slowed down the rate of spread of roe and muntjac deer relative to the baseline models (Table 3-9), and made their predicted distributions much patchier (Figure 3-13). The inclusion of DVCs significantly decreased the performance of roe and muntjac deer models (Table 3-9), and no DVCs were predicted in the red deer models. This is a result of the relatively low number of deaths (*c.*740 DVCs, see page 59) observed each year, which translated into very low predictions of DVCs across the whole of the U.K. I chose to account for the spatial distribution of roads, and therefore DVCs, rather than decreasing the survival rate of all individuals across the whole modelling landscape irrespective of whether the dispersing individuals would come into contact with a road (as Jennings 2009 did). The methodology used here to account for DVCs provides a coarse first attempt in incorporating DVCs into a SEPM in a more realistic way. However, the methodology used in this chapter can undoubtedly be improved if and when more detailed data on the date and location, as well as the number, sex and species of deer involved in DVCs are recorded in a more rigorous way. Undoubtedly, more sophisticated methodology to account for DVCs in SEPMs can and should be developed once such data are available.

By changing survival and fecundity rates across a range of plausible values (Table 3-4) I was able to determine which of those parameters significantly influenced model performance. Changing fecundity had little effect on the performance of models for

the three focal species (Figure 3-10, Figure 3-11 and Figure 3-12). However, survival had a relatively strong effect (Figure 3-10, Figure 3-11 and Figure 3-12). This finding accords with SEPMs for a range of diverse organisms, including plants (Travis et al. 2011) and brown bears (Wiegand et al. 2004b). I found that adult survival was the most influential parameter acting on the performance of muntjac (Figure 3-11), and red deer (Figure 3-12) models, while juvenile survival had the strongest influence on the performance of roe deer models (Figure 3-10). Nonetheless, for all species, model performance was generally maximised when using high juvenile and adult survival rates. Accordingly, it is likely that factors which increase survival rates, such as increased resource availability in response to changing climates (Albon et al. 1983, Moyes et al. 2011), will also facilitate an increased rate of spread, and *vice versa*. While this study was focussed on three British species, it is likely that survival has a strong influence on the speed of spread of other deer species with similar ecologies; given the flexibility of the SEPM, this assumption could be tested in the future. The survival rates included in the SEPM were kept static across the 35 years of simulation (as in e.g. Rushton et al. 1996), and therefore care must be taken in the interpretation of my results. Again, the flexibility of the model will permit its use in testing how dynamic management of deer over small geographic areas or time scales (likely for management scenarios) will impact on their spread.

A next step in improving the SEPM would be to account for how parameters such as sex ratio, fecundity, and survival may change both spatially and temporally as a result of factors including interspecific competition, climate variation (Gaillard et al. 1997), and the indirect costs of dispersal (Travis et al. 2012) such as costs of settlement in new areas (Bonte et al. 2012). While studies have documented changes in sex ratio, litter size and survival in response to population density and environmental conditions (e.g. Hewison 1996, Hewison and Gaillard 1996, Putman et al. 1996, Clutton-Brock et al. 1997, Gaillard et al. 1997, Clutton-Brock et al. 2002, Pettorelli et al. 2003, Nilsen et al. 2009), these tend to be focussed on single or neighbouring populations. Currently, there are insufficient data to account for these relationships across large temporal and spatial scales such as the one studied here. It would also be beneficial to explicitly account for inter-specific competition in the model (Staines et al. 1998, Kearney and Porter 2009). For example, theoretical and empirical studies have already shown that,

when resources are limited, muntjac deer have a competitive advantage over the native roe deer (Hemami et al. 2004, Hemami et al. 2005, Acevedo et al. 2010). However, given the high variability and complex network of such interactions between species, the strength and pattern of inter-specific competition is difficult to quantify, and has not yet been accounted for in spatially-explicit mechanistic models (but see e.g. Anderson et al. 2002, Heikkinen et al. 2007 for examples in correlative SDMs).

While it would be beneficial to capture changing vegetation dynamics (Holt et al. 1995) in the modelling procedure, such data (which would be used to create the habitat suitability maps [Chapter 2]) are not available for the study area and time periods concerned. Consequently, the habitat suitability layer used in the SEPM remained the same throughout the modelling procedure. While habitat suitability is unlikely to have changed dramatically between years, it is likely that habitat suitability between the years 1972, the model start, and 2007, the model end, had altered gradually over time, as a result of, for example, changes in climate, agricultural practices and an increase in woodland planting. However, until data on habitat cover is collected in a systematic way, and at regular (ideally yearly) time periods, predictions from models such as the one described in this chapter will be constrained to assumptions of static habitat suitability and availability.

In this chapter I have presented and tested a SEPM that can be used to model the distribution of species across a heterogeneous environment. The very nature of modelling requires that a balance is made between limiting data demands of the model and incorporating enough data to reflect reality (Radeloff et al. 1999, Travis et al. 2011). Ideally the SEPM would take into account spatial and temporal variation in parameters, or at least be parameterised using data from a large, representative sample of populations (Kearney and Porter 2009). This latter point could be particularly pertinent when interpreting the results of the muntjac deer models, as data on demographic rates for this species were relatively scarce (Appendix 2). While this chapter is focussed on modelling deer distributions, by incorporating species-specific traits such as survival- and dispersal rates, the model has been adapted to simulate the spread of butterflies (Kerr 2012). The SEPM can also be projected onto other landscapes, and into the future. Despite the limitations described above, the SEPM performed well in retrodicting the spread of deer and, as a result, I use the

model in the following chapter to predict the future distributions of these species in Britain.

Chapter 4 : Predicting the potential future distributions of roe, red and muntjac deer in Britain

4.1. Abstract

Background: Given the economic, cultural and ecological importance of deer, it is surprising that spatially-explicit predictions of how their distributions may change in the future are extremely rare. Here, I present the first attempt to predict the future distribution of deer in Britain using a mechanistic, spatially explicit modelling approach.

Methodology: I use the SEPM developed and validated in Chapter 3 to predict the distribution of roe *Capreolus capreolus*, muntjac *Muntiacus reevesi* and red deer *Cervus elaphus* in Britain from 2007 to 2040.

Findings: Roe deer are predicted to occupy 92% of Britain by 2040, while red and muntjac deer are predicted to nearly double their distribution sizes between 2007 and 2040 (muntjac: from 29% to 55%; red deer: 43% to 74%). Most strikingly, the SEPM predicts that overlap between the non-native muntjac deer and both roe and red deer will increase from an observed 6% in 1972, to 57% by 2040.

Conclusions: All three species are predicted to continue to increase their ranges in the future. This modelling approach will be a useful tool both in highlighting the locations where increased deer management may be required in the future, and in testing how different management strategies may influence the future rate and pattern of spread.

4.2. Introduction

To date, correlative species distribution models (SDMs) have been the primary methodology used to predict the potential future distribution of species (Huntley et al. 2010). Examples include studies of plants (Franklin et al. 2013), fishes (Chu et al. 2005), invertebrates (Hill et al. 2002), amphibians and reptiles (Araujo et al. 2006), birds (Huntley et al. 2008), and mammals (Thuiller et al. 2006a, Levinsky et al. 2007, Acevedo et al. 2011). In general, these studies either assume that a species will be able to completely track future environmental changes (unlimited dispersal, e.g. Thuiller et al. 2006a, Levinsky et al. 2007), or fail to track environmental changes completely (no dispersal e.g. Hill et al. 2002, Araujo et al. 2006) (Midgley et al. 2006). Both scenarios offer a simplistic view of how distributions may change, with reality likely to fall between the two (Araujo et al. 2006).

The predictions of potential future distributions obtained from correlative SDMs can be refined by using information relating species' tolerances to environmental conditions (e.g. Kearney et al. 2008, Kearney and Porter 2009, Elith et al. 2010). Even better, by making mechanistic models spatially explicit, and by incorporating range-limiting processes (Willis et al. 2009), predicted future distributions are likely to become more realistic (Huntley et al. 2010). Despite this acknowledgement, while spatially explicit population models (SEPMs) have been used to model present-day or past distributions of species (e.g. Pulliam et al. 1992, Collingham et al. 1996, Rushton et al. 1996, Rushton et al. 1997, Chapter 3, Willis et al. 2009, Marucco and McIntire 2010), they have rarely been used to predict future distributions (but see, for example, Lurz et al. 2001, Anderson et al. 2009, Marucco and McIntire 2010) or future population viability of species (Linkie et al. 2006, Keith et al. 2008).

Deer populations have been increasing in abundance and range across the world over recent decades (Côté et al. 2004, Dolman and Waber 2008), and are expected to continue to expand in the future (Fuller and Gill 2001, Ward 2005, Ward et al. 2008). As a result, overlap, and therefore competition (Johnson et al. 2000, Focardi et al. 2006, Marshal et al. 2008, Richard et al. 2010), genetic introgression (Abernathy 1994, Jepsen et al. 2002), and spread of disease (Dolman and Waber 2008) between sympatric deer species is also likely to increase (but see Bartos et al. 2002, Ward 2005).

However, predictions of the future distributions and overlap between deer are extremely rare in the literature and those that are published have used correlative modelling approaches (Chapman et al. 1994, Acevedo et al. 2011). Additionally, both of these studies did not threshold predicted habitat suitability values to predict the potential future presence/absence of deer in Britain. As such, there is clearly a need for information on the potential future rate and pattern of spread; this information would be invaluable in helping to guide the conservation and management of deer (Pompilio and Meriggi 2001).

In this chapter I use the spatially-explicit population model developed and validated in Chapter 3, to predict the potential future distribution of red, roe and muntjac deer in Britain. I discuss predicted changes in spatial distribution and range extent, and quantify the potential changes in overlap between deer distributions. Finally, I compare my results to previous predictions of range increases (Ward 2005), and discuss my findings in relation to deer management.

4.3. Methods

4.3.1. Predicting the potential future spread of deer between 2007 and 2040

Parameter estimates used in the baseline models for red, roe and muntjac deer are shown in Table 4-1 (and have been discussed in detail in Chapter 3 and Appendix 2). Models of potential future distribution were seeded using the most comprehensive and up-to-date deer distribution data available, from 2007 (Figure 2-1, page 28), and were run into the future to obtain estimates of spread to 2040. This time scale was chosen as being appropriate because model predictions were previously validated across a 35-year time period (Chapter 3), which is a comparable duration. To account for stochasticity among model runs, each model was run 30 times.

The percentage increase in range sizes between the present day (classed as 2007) and the future (2020 and 2040) was calculated, as well as the percentage of Britain predicted to be occupied by each species. Ward (2005) used observed rates of expansion of British deer between 1972 and 2002, to predict the potential future range extents in 2007 and 2012. I compared my predicted extents of occurrence in

2012 to Ward's (2005) predictions of range increases, and as observed data for 2007 are now available, I was also able to compare his predictions to observations in that year. Compound annual increase in range between 2007 and 2020, and between 2020 and 2040 was calculated using Equation 1-a, and compared to observed compound annual rates of increase between 1972 and 2007 (Table 1-2).

Table 4-1. Parameter estimates used in models to predict the spread of roe deer, muntjac deer, and red deer in Britain, discussed in Chapter 3 and Appendix 2.

		Baseline value (species)		
Parameter	Description	Roe	Muntjac	Red
SurvA	Probability of adult survival	0.95	0.86	0.95
SurvJ	Probability of juvenile survival	0.83	0.75	0.69
pBreedAdult	Probability of successful breeding (adults)	0.81	1.00	0.90
pBreedJuvenile	Probability of successful breeding (juveniles)	0.66	0.60	0.50
MaxK	Maximum carrying capacity	19	35	27
DispersalSteps	Maximum number of dispersal steps	20	13	31
pOptDisp	Probability of optional dispersal	0.05	0.05	0.00
pSingleton	Probability of producing a single offspring	0.27	1.00	1.00
pTwin	Probability of producing twins	0.72	n/a	n/a
birthSexRatioSingleton	Birth sex ratio of singleton offspring	0.60	0.50	0.55
birthSexRatioTwin	Birth sex ratio of twin offspring	0.51	n/a	n/a
birthSexRatioTriplet	Birth sex ratio of triplet offspring	0.50	n/a	n/a
AgeFirstBreed	Age at first breeding	1	1	2
No.Generations	Number of time steps the model will run over	33	50	33
numberofSeedCells	Number of 1km^2 cells to seed population in (of 100 possible cells)	10	90	10

As there is evidence for competition between deer species (see *Introduction*), the degree of overlap between the past (1972 and 2007) and potential future (2020 and 2040) distributions of deer was also calculated. Overlap between the ranges of non-native (muntjac deer) and native species (either roe or red deer) was expressed as a percentage of the native species' range. Overlap between red and roe deer was expressed as percentage of roe deer range, given that red deer outcompete roe deer (Latham et al. 1999).

4.4. Results

4.4.1. Potential future distribution of red, roe and muntjac deer

Assuming that environmental suitability for deer in the future remains the same as at present (because I was constrained to using a static habitat suitability layer), it is predicted that the potential future distribution of roe, muntjac, and red deer in 2040 will increase – relative to their observed distributions in 2007 – by 29%, 91% and 74%, respectively. For red and muntjac deer, the annual rate of increase to 2020 is predicted to be faster than the observed rates of increase between 1972 and 2007; roe deer are predicted to experience a reduced rate of increase to 2020, and for all species, the rate of increase is predicted to slow quite dramatically to less than 1% per year between 2020 and 2040 (Table 4-2).

Table 4-2. Observed (1972 to 2007) and predicted (from 2007) annual rates of range expansion of roe, muntjac and red deer, calculated using Equation 1-a.

	Compound annual increase in range (%)		
Species	1972 - 2007	2007 - 2020	2020 - 2040
Roe	2.3	1.7	0.2
Muntjac	3.5	4.0	0.7
Red	1.8	3.3	0.6

All three species had increased their range sizes by 2007 even more than was predicted by Ward (2005) (Table 4-3). Strikingly, roe deer are predicted to occupy 92% of 10km^2 grid squares in Britain by 2040 (Figure 4-1; Table 4-3) increasing their distribution into Wales, central England, and Kent; only a few grid squares on the Scottish islands are predicted to remain unoccupied by that time, as well as a few locations between Somerset and Surrey (Figure 4-1).

Table 4-3. Observed and predicted extent of occurrence of roe, muntjac red deer across Britain (as a percentage of 2847 10km^2 grid squares across Britain). Sources relate to predictions made by Ward (2005) (PW), observed distributions (O), and predictions from the SEPM for each species (P). The mean (± SD) number of 10km^2 grid squares predicted to be occupied in 2020 and 2040 from 30 model runs are shown.

	% Britain (number of 10km^2 grid squares)			
Species	2007 (PW)	2007 (O)	2020 (P)	2040 (P)
Roe	62 (1762)	71 (2032)	89 (2538 ± 4)	92 (2629 ± 3)
Muntjac	24 (693)	29 (824)	48 (1364 ± 3)	55 (1570 ± 3)
Red	23 (647)	43 (1211)	65 (1850 ± 7)	74 (2096 ± 6)

Red deer are predicted to increase their distribution markedly by 2040 (Table 4-3). In particular, many isolated populations in England are predicted to join up by this time period (Figure 4-1). Only a few populations, for example around Northumberland National Park, in north-west Wales and in Kent, are predicted to remain relatively isolated (in terms of number of contiguous grid squares) by 2040.

At present, muntjac have a very widespread distribution across the south of England (Figure 4-1), and are predicted to increase their extent of occurrence in Kent, south-western England, and up from northern East Anglia towards the Borders (Figure 4-1). There are a number of grid squares around Cambridgeshire, which are predicted to experience local extinctions between 2020 and 2040 (Figure 4-1). These areas coincide with counties where hunting pressure was also modelled to be high (Figure 3-6).

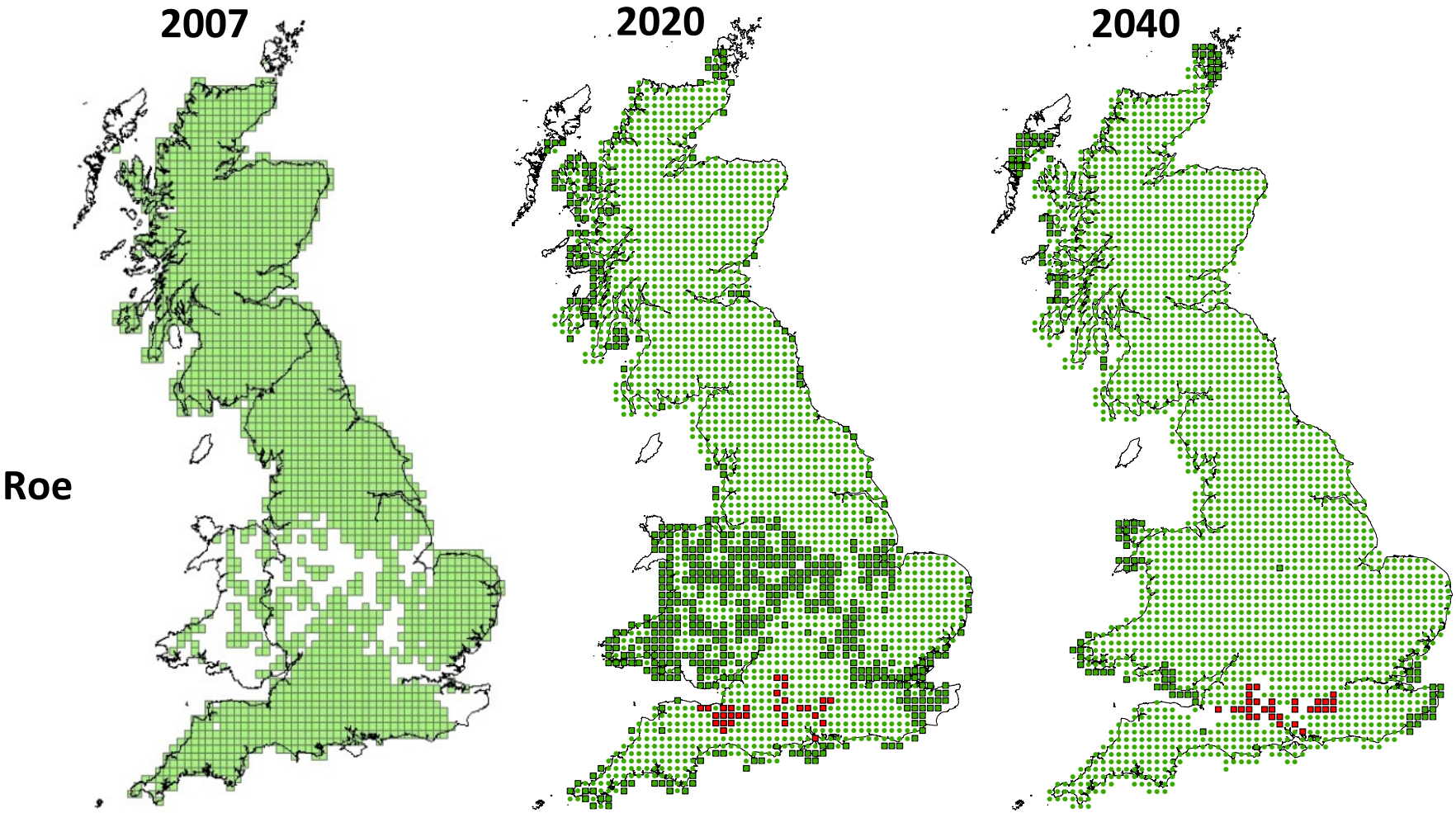


Figure 4-1. Observed (2007) and predicted future (2020 and 2040) distribution of roe, muntjac and red deer in Britain at a 10km^2 resolution. Dark green squares in the latter two years (2020 and 2040) represent grid squares colonised between the focal and earlier time period. Red squares in the latter two years represent grid squares where the focal deer species have become locally extinct between the current and earlier time period. Continued overleaf.

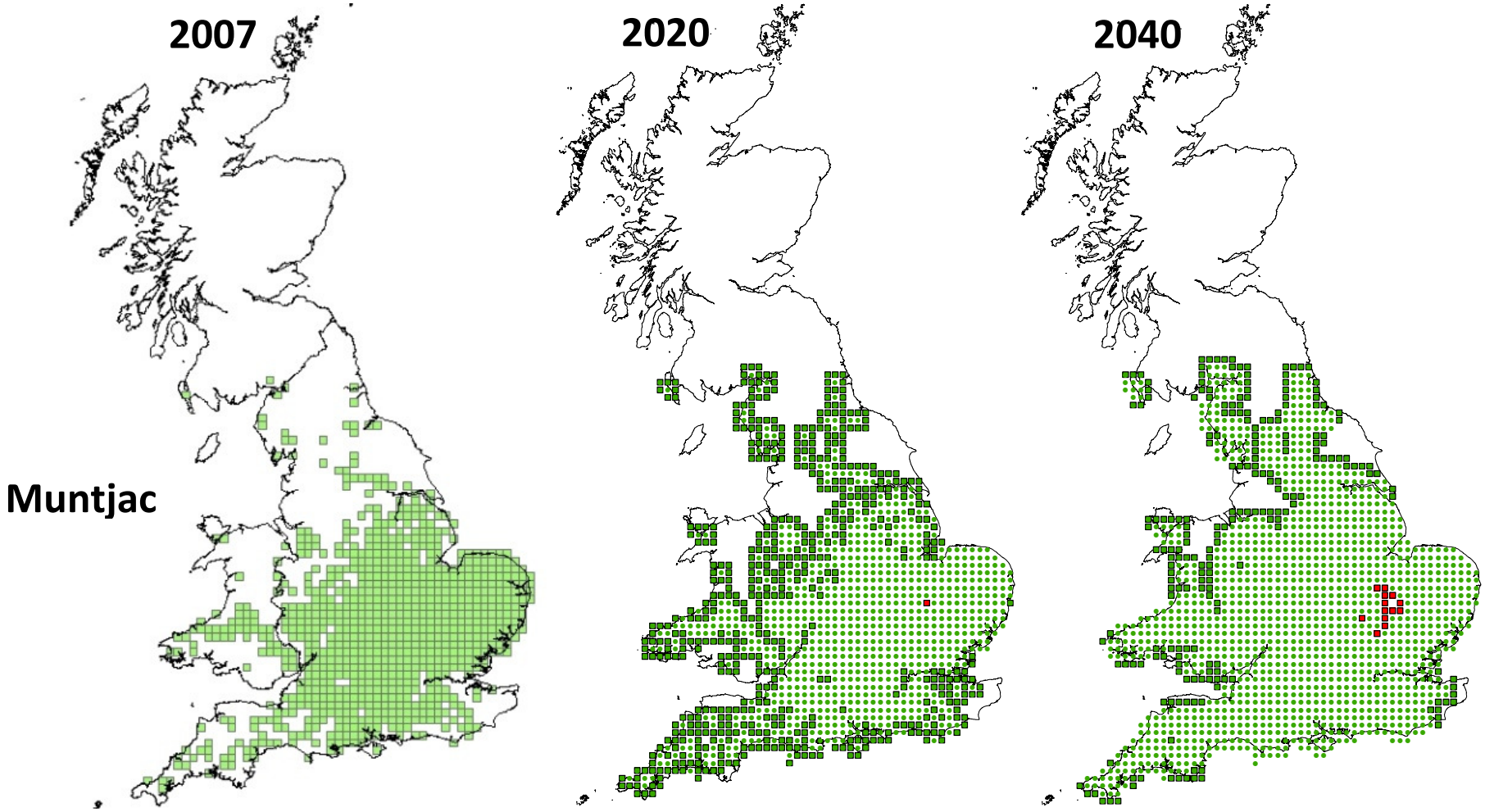


Figure 4-1 continued. Figure continued on the next page.

Red

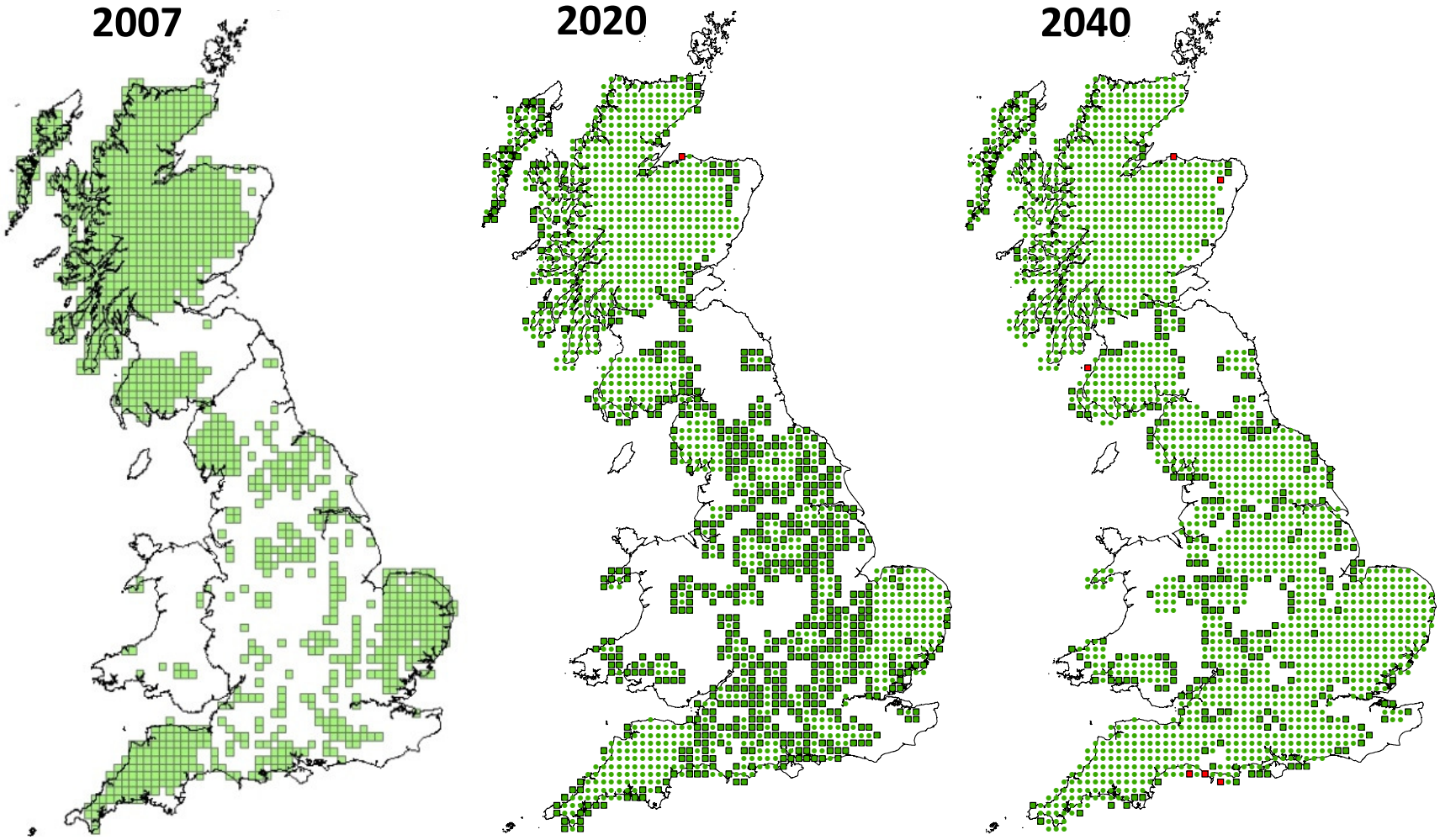


Figure 4-1 continued.

4.4.2. Observed and predicted overlap between red, roe and muntjac deer ranges

Overlap between species' ranges was predicted to increase over time (Table 4-4). However, in comparison with earlier time periods, the rate of overlap increase is predicted to slow down between 2020 and 2040 (Figure 4-2; Figure 4-3). The most dramatic increases in overlap were predicted between the non-native muntjac deer and the native deer species (roe [Figure 4-3b] and red deer [Figure 4-3c]). In 1972 muntjac deer occupied 6% of both roe and red deer ranges, and by 2040 this overlap is predicted to increase to 57% (Table 4-4). Between 1972 and 2040, observed overlap between roe and red deer ranges was predicted to nearly double from 41% in 1972, up to 76% of roe deer range in 2040 (Table 4-4; Figure 4-3a).

Table 4-4. Observed (in 1972 and 2007) and predicted (in 2020 and 2040) overlap between deer species ranges. Overlap between the ranges of non-native (muntjac deer) and native species (either roe or red deer) is expressed as a percentage of the native species' observed range in 1972 and 2007, or predicted range in 2020 or 2040 (see Table 4-3). Overlap between roe and red deer is expressed as a percentage of roe deer range. Predictions are mean percentage overlap from 30 replicates. Also provided are the sum (± SD) of $10km^2$ across Britain where the two species overlap, in each of the four time periods.

		% overlap (number of $10km^2$ grid squares)			
Species		1972	2007	2020	2040
Roe	Red	41 (371)	53 (1081)	68 (1738 ± 7)	76 (1986 ± 7)
Roe	Muntjac	6 (51)	31 (638)	52 (1311 ± 5)	57 (1511 ± 4)
Red	Muntjac	6 (42)	26 (315)	50 (923 ± 5)	57 (1186 ± 6)

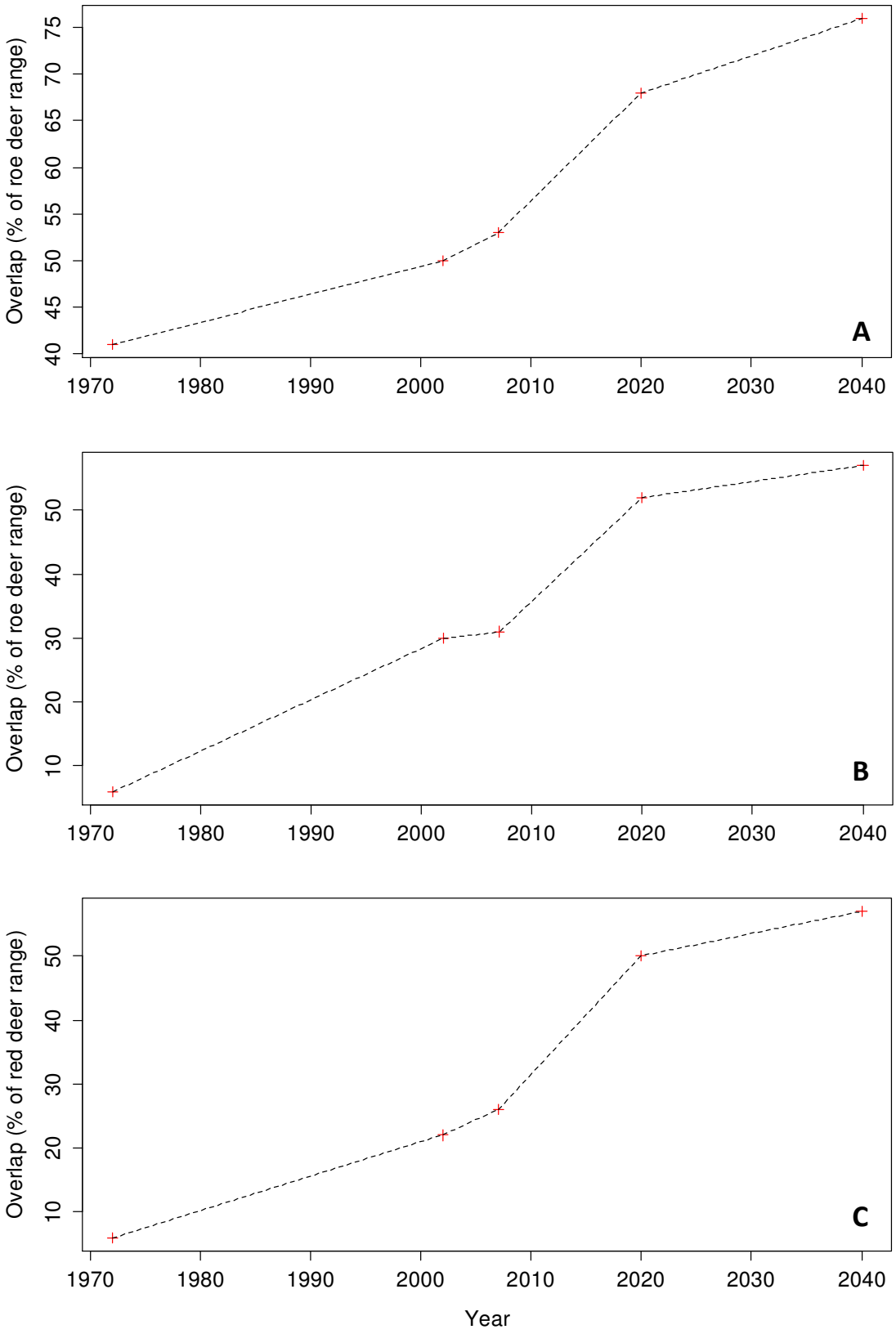


Figure 4-2. Overlap between roe and red deer (A), roe and muntjac deer (B) and red and muntjac deer (C) ranges between 1972 and 2040. Values from 2007 are mean predictions from the SEPM (each model was run 30 times for each species individually, and then mean overlap between ranges calculated). Overlap is expressed as a percentage of roe (A and B) or red (C) deer ranges, as discussed in the methods section.

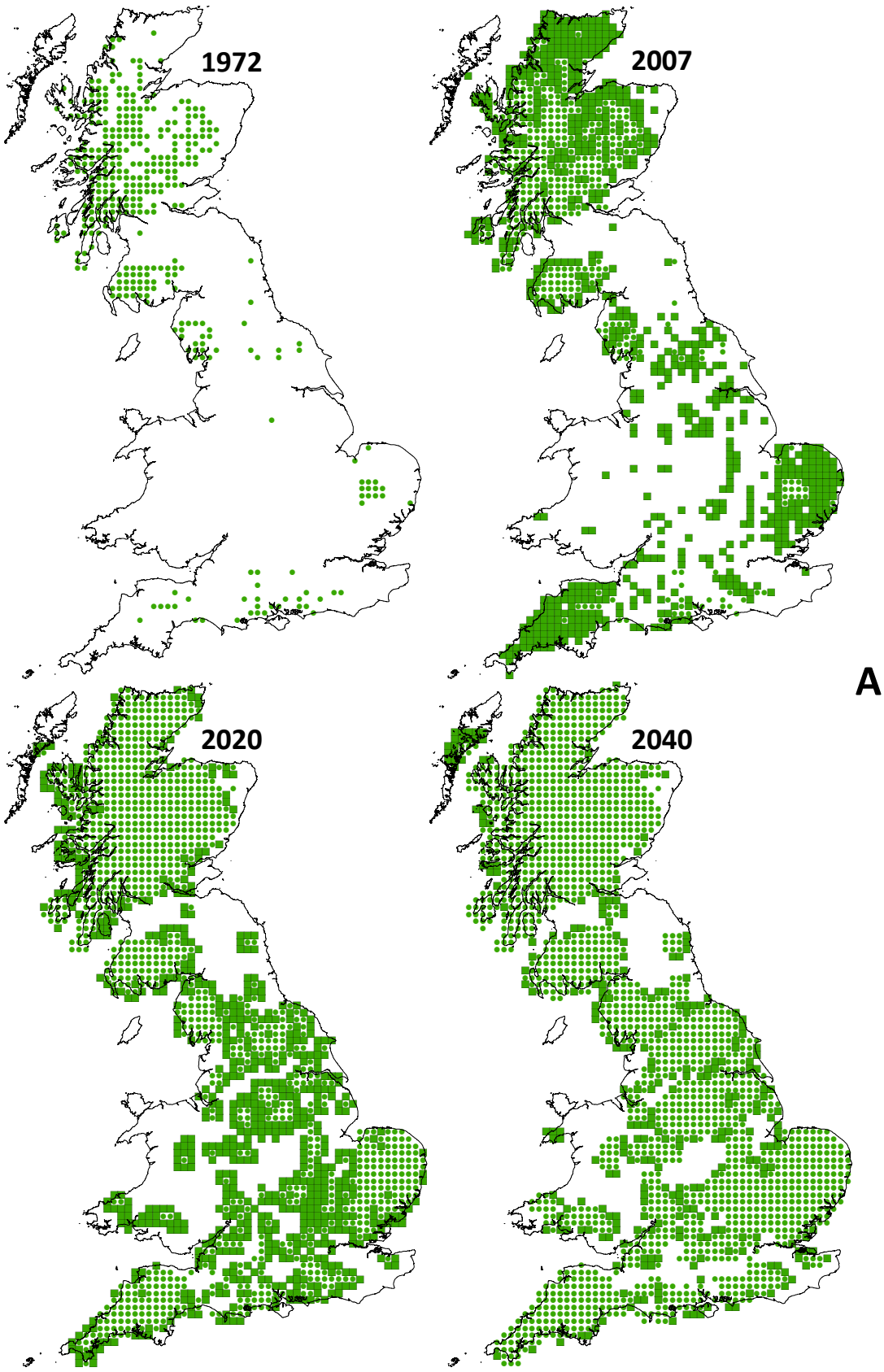


Figure 4-3. Observed and predicted overlap between roe and red deer ranges (A), roe and muntjac deer ranges (B), and red and muntjac deer ranges (C) in 1972, 2007, 2020, and 2040 at 10km^2 resolution. Green squares show areas of novel overlap, and green circles show areas of existing overlap between the focal time period and the previous time period. Figure continued on the next page.

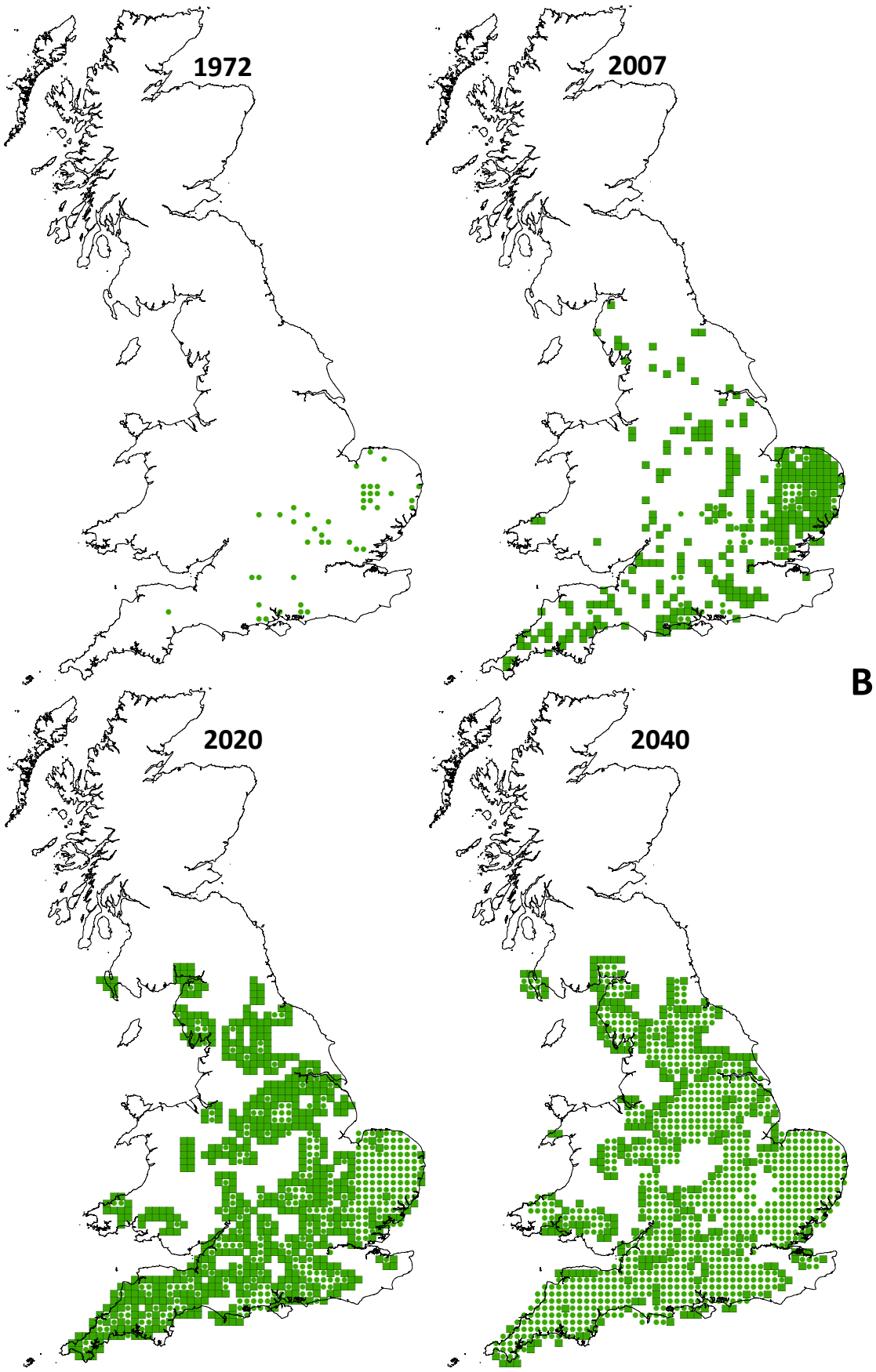


Figure 4-3 continued. Figure continued on the next page.

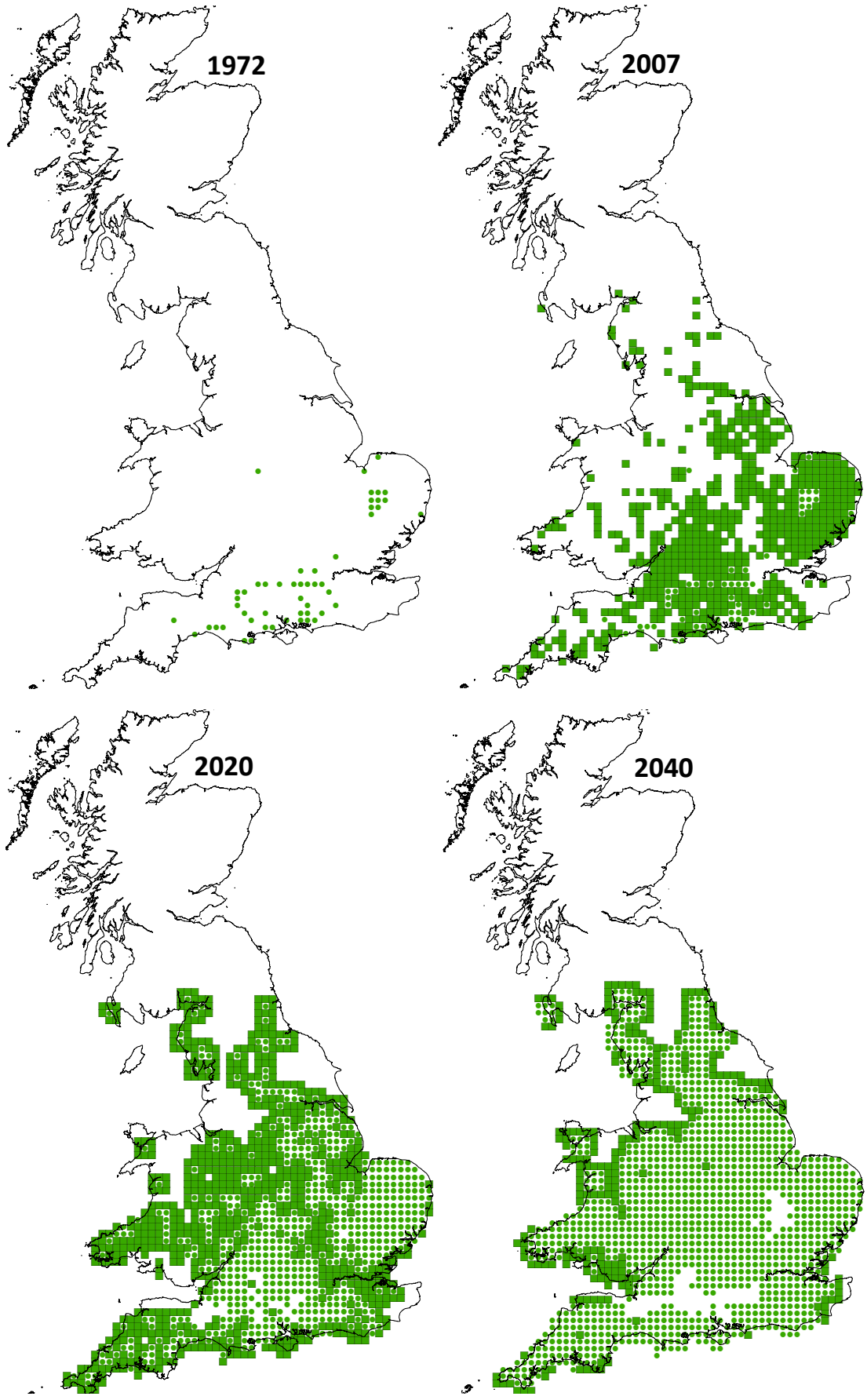


Figure 4-3 continued.

4.5. Discussion

Here, I provide the first attempt to predict the future distributions of British deer using a spatially explicit mechanistic model. It is predicted that roe deer will increase their distribution by 29% (relative to their observed distribution in 2007) and will occupy the vast majority of Britain by 2040 (Table 4-3), increasing their ranges mainly in Wales and the midlands (Figure 4-1). Their rate of increase was lower than for the other two species (Table 4-2), which is most likely because roe deer have proportionally less space left to expand into (Putman and Moore 1998, Ward 2005). Red deer are predicted to occupy nearly three-quarters of Britain by 2040 (Table 4-3). Given their widespread, uniform, current distribution in Scotland, the main areas of increase in distribution are predicted to be in England (Figure 4-1). The barrier for red deer across the central belt of Scotland, which was identified by Ward (2005), is also evident in my predictions, adding support for this modelling approach, and therefore its predictions.

Muntjac deer are predicted to nearly double their extent of occurrence in England and Wales by 2040 (Table 4-3). The northwards pattern of spread between 2007 and 2040 was similar to that predicted by Chapman *et al.* (1994). However, by 2007 muntjac had already exceeded the range predicted by these authors; the observed spread into Devon and Cornwall which was predicted by the SEPM (Figure 4-1) was not predicted by those authors. The predicted future distribution of muntjac deer was more restricted than the predicted presence/absence obtained by correlative SDMs developed using abundance data in Chapter 2. Using the SEPM, muntjac were not projected to reach areas predicted to be environmentally-suitable in northern England and Scotland (abundance model: Figure 2-2, page 33). This highlights the fact that by incorporating demographic and range-limiting processes in to models, more realistic estimates of spread can be obtained.

Given the predicted increases in range size of all three species (Table 4-3), it is unsurprising that the overlap between their distributions is also expected to increase over time (Table 4-4; Figure 4-2). Muntjac deer are predicted to occupy 57% of red and roe deer ranges by 2040. This is particularly pertinent for the roe deer given the high overlap with muntjac deer in their habitat and dietary requirements. As such, it is possible that efforts to reduce muntjac deer numbers through alteration of habitat

would, inadvertently, simultaneously reduce roe deer abundances. Equally, improving habitat for the native roe deer would be of benefit to the non-native muntjac deer, and may even result in roe deer being displaced in those areas (Acevedo et al. 2010). The overlap between the native red and roe deer is also predicted to increase over time (to 76% in 2040, from the observed value of 53% in 2007). When resources are limited, this may have detrimental effects on the abundance of roe deer , given that red deer have been shown to outcompete this species under such conditions (Latham et al. 1999, Richard et al. 2010).

A number of improvements could be made to the SEPM (if data were available), but a number of limitations must also be considered too. As discussed in Chapter 3, I was unable to account for potential future environmental change as well as hunting pressure given that predictions of these changes are not available. Additionally, in Chapter 3 I showed that the spread of deer is influenced by both juvenile and adult survival (Figure 3-10, Figure 3-11 and Figure 3-12). In this chapter I used baseline values for survival parameters (Table 4-1) as it is unclear how survival rates may change temporally and spatially in the future. However, in areas where resource availability is likely to increase in the future (resulting from, for example, an increased growing season length), it is expected that the survival and reproductive success of female deer will also increase (see Moyes et al. 2011 for review). In this eventuality, it is likely that the rates of range expansion reported here will be underestimates (as increasing survival rate increases spread of deer; see Figure 3-10, Figure 3-11 and Figure 3-12). However, other factors will also interplay to influence the survival of deer, and therefore their spread. For example, if resource availability increases, population density is likely to increase. In turn, overlap and competition between deer species will increase, which may have negative feedbacks, particularly for species such as the roe deer (Hemami et al. 2004, Hemami et al. 2005, Acevedo et al. 2010).

In this chapter I have shown that the predicted distributions of red, roe and muntjac deer are expected to continue to increase in the future (Figure 4-1; Table 4-3), and that overlap between the distributions of these three species is also likely to increase (Table 4-4). Model results have highlighted areas where overlap and therefore competition between species is likely to increase (e.g. in southern Wales, and Kent), and/or where spread into novel areas is predicted (solid squares in Figure 4-1). Given the concerns

regarding inter-breeding between red and sika deer (Abernathy 1994, Goodman et al. 1999, Senn et al. 2010), an extension of the model could be used to identify locations where the distributions of sika deer and red deer will overlap in the future.

While this chapter has been focussed on deer species in Britain, similar SEPMs could be used to predict the future distribution of ungulate species which are increasing in range and abundance elsewhere, such as the white-tailed deer in America. Equally, the model could be used to identify factors which might aid the management and recovery of range-restricted or declining species, such as the Père David's deer *Elaphurus davidianus* in China (www.iucnredlist.org/details/7121/0, accessed 29th June 2013).

Although mechanistic models require detailed knowledge of a wide range of parameters that limit distributions (Guisan and Thuiller 2005), by including these data, SEPMs can be used to make more robust predictions of range shifts than correlative models alone (Kearney and Porter 2009). The input data and parameter estimates should be modified, and the predictions checked, as and when more information is acquired (Conroy et al. 1995). Furthermore, model structure should also be adapted as conditions – such as management and/or efforts to reduce DVCs – change (Conroy et al. 1995). This will improve the reliability of predictions, allow for adaptive management strategies, and enhance our understanding of how and why species distributions may change in the future (Conroy et al. 1995, Marucco and McIntire 2010). In particular, proactive management based on robust predictions of how species ranges may change in the future would be beneficial in, for example, identifying the locations where: mitigation against DVCs may be required or need to be increased; densities of deer are predicted to become extremely high and therefore where diseases such as tuberculosis among deer, and therefore among farmed livestock (although deer-livestock transmission has not explicitly been investigated [www.bds.org.uk/response_to_defra, accessed October 2013]), may increase; or where sensitive species such as understorey birds may benefit from increased deer management such as the installation of exclosures or increased culls.

Chapter 5 : The relationships between roe deer density and vegetation structure, abundance and composition in English woodlands

5.1. Abstract

Background: A large body of literature reports the negative, cascading effects of deer on vegetation structure, diversity and abundance; those studies are generally undertaken in a small number of sites, with multiple deer species, and using exclosures. By collecting data from a large number of sites encompassing a range of natural deer densities, and without the use of exclosures, I investigated the impacts of roe deer on vegetation abundance, diversity and density.

Methodology: I collected vegetation data from 35 woodland sites across Great Britain during 2011 and 2012. An index of roe deer density in each site was calculated using count data collated as part of the British Trust for Ornithology's Breeding Bird Survey scheme. I then used beta regression and generalised linear models to investigate the relationships between three vegetation metrics (abundance, diversity and density) and the index of deer density.

Findings: Shrub layer vegetation cover ($F_{1,33}$ = 6.67, p < 0.05) and shrub layer vegetation diversity (Z = -2.51, p < 0.01) decreased linearly with increased roe deer density. Mean shrub layer cover decreased from 49% in sites with no deer, to 32% in sites with the highest deer density. The data provided no support for a relationship between deer density and: ground layer vegetation diversity (Z = -0.75, p = 0.45), ground layer vegetation cover ($F_{1,33}$ = 0.14, p = 0.71), or vegetation density (0 – 50cm from the ground: Z = -0.85, p < 0.40; 51 – 100cm : Z = -0.68, p < 0.50, 101 – 150cm: Z = -0.70, p = 0.49, 151 – 200cm: Z = -0.72, p= 0.47).

Conclusions: The abundances of roe deer are expected to increase in the future – in areas where this occurs, the abundance and diversity of shrub layer vegetation is likely to decrease. My results suggest that increased herbivory by roe deer could have wide-ranging, cascading impacts on species that depend on the shrub layer for food, cover or nesting opportunities.

5.2. Introduction

Browsing and grazing by deer is a natural process, which has always played a role in determining the structure and composition of woodland systems (Putman and Moore 1998). However, where deer spread into new areas, and/or increase in abundance, there is potential for an increase in negative impacts on the environments they inhabit (Dolman et al. 2010). Indeed, in recent years there has been growing concern regarding the potential cascading effects deer may have on components of biodiversity, from vegetation such as the native bluebell *Hyacinthoides non-scripta* to invertebrates, birds such as nightingales, decomposers, and small mammals (Pollard and Cooke 1994, Putman and Moore 1998, Gill 2000, Rooney and Waller 2003, Côté et al. 2004, Wardle and Bardgett 2004, Allombert et al. 2005a, Greenwald et al. 2008).

Over recent decades British deer populations have been increasing in both range and abundance (Fuller and Gill 2001, Ward 2005, Ward et al. 2008), and it is clear that the number of deer culled per year must increase if we want to keep populations in check (P.O.S.T. 2009). Roe deer populations have increased from an estimated 500,000 deer in 1995, to approximately 800,000 in 2009 (Harris et al. 1995, P.O.S.T. 2009), and their ranges increased by over 5% year-on-year between 2003 and 2007 (Ward 2005, Ward et al. 2008).

Studies in Britain have shown that as the density of deer increases, there is a reduction in the density (Joys et al. 2004, Gill and Fuller 2007, Gill and Morgan 2010) and diversity (Putman et al. 1989, Gill and Beardall 2001) of woodland vegetation, and an increase browsing damage to individual plants (Kay 1993, DeGabriel et al. 2011). Many authors have reported impacts of deer browsing on individual plant species: decreases in the abundance of heather (Baines et al. 1994, DeGabriel et al. 2011), dog's mercury *Mercurialis perennis* (Cooke et al. 1995), bluebell (Cooke 1997, Cooke et al. 2004), bramble, honeysuckle, holly and ivy (Putman et al. 1989, Kirby 2001) have been recorded in response to deer browsing in the U.K. Conversely, several studies have reported an increase in the cover of grasses (Baines et al. 1994, Gill and Fuller 2007), ground ivy, sedges, ferns (Gill 1992b, Kirby 2001), and on fast-growing plants such as meadowsweet *Filipendula ulmaria* and wild angelica *Angelica sylvestris* (Kirby 2001), as an indirect effect of increased deer browsing. All of these studies were in

multi-deer-species environments, where the relative contributions of deer species could not be quantified. To my knowledge, very few studies have looked exclusively at the effects of roe deer in woodlands (but see e.g. Ballon et al. 1992, Morellet et al. 2001, Sage et al. 2004). However, even in these studies, other deer species were documented as being present, but their impacts were not quantified. Furthermore, these studies were focussed within single sites. To my knowledge, Ballon *et al.'s* (1992) study is the only UK-based study investigating the impacts of roe deer on vegetation. These authors used paired exclosure/control plots within woodlands in one site in Dorset, where roe density in control plots was kept constant at approximately 9km^{-2}. This study found that herbivory by roe deer negatively affected plant species composition and density. These negative impacts were attributed solely to roe deer despite fallow deer also being recorded on the estate during one of the surveys. Consequently, the presence of fallow deer may have confounded their results, given the severe, localised damage this large-bodied, herding species can cause (Moore et al. 1999).

Most studies assessing impacts of deer on vegetation have been undertaken using exclosure or artificial-stocking experiments (e.g. Ballon et al. 1992, Baines et al. 1994, Cooke et al. 1995, Cooke 1997, McShea and Rappole 2000, Morecroft et al. 2001, Stone et al. 2004, Kleintjes Neff et al. 2007). While exclosure studies provide insights into the effects deer have upon their environment, they do not always reflect what would occur naturally (Allombert et al. 2005a), and generally only provide comparisons between impacts in areas of high deer density, and where deer are absent. It has been suggested that intermediate levels of browsing are optimal for the management and conservation of biodiversity (Wäber 2010). Thus, understanding how impacts differ across a range of deer densities and therefore grazing intensities is advocated (Hester et al. 2000). Despite this suggestion, few studies have assessed the impacts of deer on vegetation across sites encompassing a range of different deer densities. Examples of those that have include the work by Horsley *et al.* (2003) who found negative, linear relationships between white-tailed deer density and overall plant species richness, as well the abundance of individual tree species such as red maple *Acer rubrum*, and American beech *Fagus grandifolia*. Positive relationships were found between deer density and the percentage cover of ferns and grasses. More recently, Nuttle *et al.*

(2014) showed that high white-tailed deer densities (up to 31km^{-2}) in the first ten years of woodland establishment had profound, long-term impacts on vegetation composition and density, even when deer densities were managed to remain at ambient levels (~11km^{-2}) for the two decades following establishment. Although there are a number of British studies which have also investigated the relationships between differing deer densities and woodland vegetation metrics, these studies have focused on: red deer (Holloway 1967, Millett et al. 2006); on a combination of deer species (Gill and Morgan 2010); or on a combination of impacts of deer and sheep (Palmer et al. 2003). As such, none have explicitly investigated the impacts of the small-bodied and concentrate-selecting deer across a range of deer densities and therefore grazing intensities. Deer species composition is an important factor to consider: it is expected that the larger-bodied deer (such as the red, fallow and sika deer) will have greater impacts on vegetation than smaller-bodied species (e.g. roe, muntjac or CWD), given their differences in body size, social organisation and feeding strategies (Putman 2003, Putman et al. 2011a).

In this chapter, I collect data from 35 field sites across Britain to assess the impact of the small-bodied roe deer on woodland vegetation. The field sites encompass a range of natural roe deer densities, to allow me to investigate the relationships between roe deer density and the:

- diversity of shrub and ground-layer vegetation;
- diversity of canopy trees;
- density of shrub and ground-layer vegetation;
- abundance of shrub and ground-layer vegetation; and
- the abundance of individual plant species.

It is hypothesised that the diversity and abundance of shrub and ground-layer vegetation will be lower in sites with higher deer density as deer will have short-term, direct impacts at these vegetation heights. I investigate the shape of the relationships listed above in order to ascertain whether there is a threshold of roe deer density above which impacts would be negative. However, deer density is not the sole factor influencing woodland vegetation (Putman et al. 2011a), and for this reason I also investigate site factors which may also play a role in shaping vegetation density,

composition, abundance and diversity; these include soil characteristics, climatic factors, and canopy cover.

5.3. Methods

5.3.1. Site selection

The only large mammal density data collected in a consistent way across the U.K. are collected as part of the British Trust for Ornithology's annual Breeding Bird Survey (BBS). Consequently, roe deer occurrence data from those surveys (approximately 3200 sites monitored across the U.K. each year) were used to identify 35 woodland sites where: roe deer were the only deer species recorded, there were three or more years of deer abundance data, and permission was granted from landowners. Twenty-six sites across England were visited during May and June 2011, and a further nine sites were surveyed during May and June 2012 (Figure 5-1).

5.3.2. Roe deer densities

The BBS methodology is described in Chapter 2. BBS mammal data were used to identify woodland field sites where roe deer were the only deer species recorded, as well as sites where no deer of any species were recorded. The mean roe deer count across all years in each site was calculated to produce an index of deer abundance. Sites were chosen as those with stable deer populations (Table S 2; page 170). The mean number of roe deer seen in each site per visit (across a mean of ten years' visits [± SD of 5] per site) ranged from 0 to 6.

Hereafter, the mean abundance of deer in each field site will be referred to as 'roe density'. However, this should only be viewed as an index of the relative density of roe deer in the field sites; it is almost certainly an underestimate of actual roe density, given the low detectability of roe deer in woodland (Newson et al. 2012).

5.3.3. Site characteristics

Soil fertility for each site (at the resolution of the site) was obtained using the Soilscapes viewer of the National Soil Resources Institute, Cranfield University (www.landis.org.uk/soilscapes/, accessed 12th July 2011 and 19th June 2012). Soil

fertility values range from 1 (very low) to 5 (very high). Where a site encompassed a range of soil types and therefore soil fertilities, the mean value was calculated.

The minimum temperature for growth of trees in temperate environments such as Britain, and used as T_{base} in this study, is 5°C (Prentice et al. 1992). The number of growing degree days above 5°C (per year, averaged [mean] across data from 1986 to 2006 i.e. the most recent thirty years' data available) for each site was calculated using observed climate data from the UK Climate Projections (UKCP09) project of the Met Office (ukclimateprojections.defra.gov.uk/; accessed 18th April 2011). Growing degrees (GD) are defined as the number of temperature degrees above a base temperature where plant growth is zero, and are calculated using equation 5.1 (McMaster and Wilhelm 1997).

$$GD = \frac{T_{max} + T_{min}}{2} - T_{base} \qquad \textit{Equation 5.1.}$$

where T_{max} is the maximum daily air temperature,

T_{min} is the minimum daily air temperature,

and T_{base} is the air temperature below which plant growth is zero.

The GD value is summed across the year to give growing degree days (GDD) per site.

A correlation matrix was used to determine significant correlations between potential predictor variables. As a result of this exploratory analysis, GDD5 was chosen as the sole bioclimatic predictor, given the strong link between GDD and the physiology and growth of plant species (Prentice et al. 1992), and because of the significant correlation with other bioclimatic variables (mean temperature of the coldest month (MTCO) and summer precipitation) (Table 5-1).

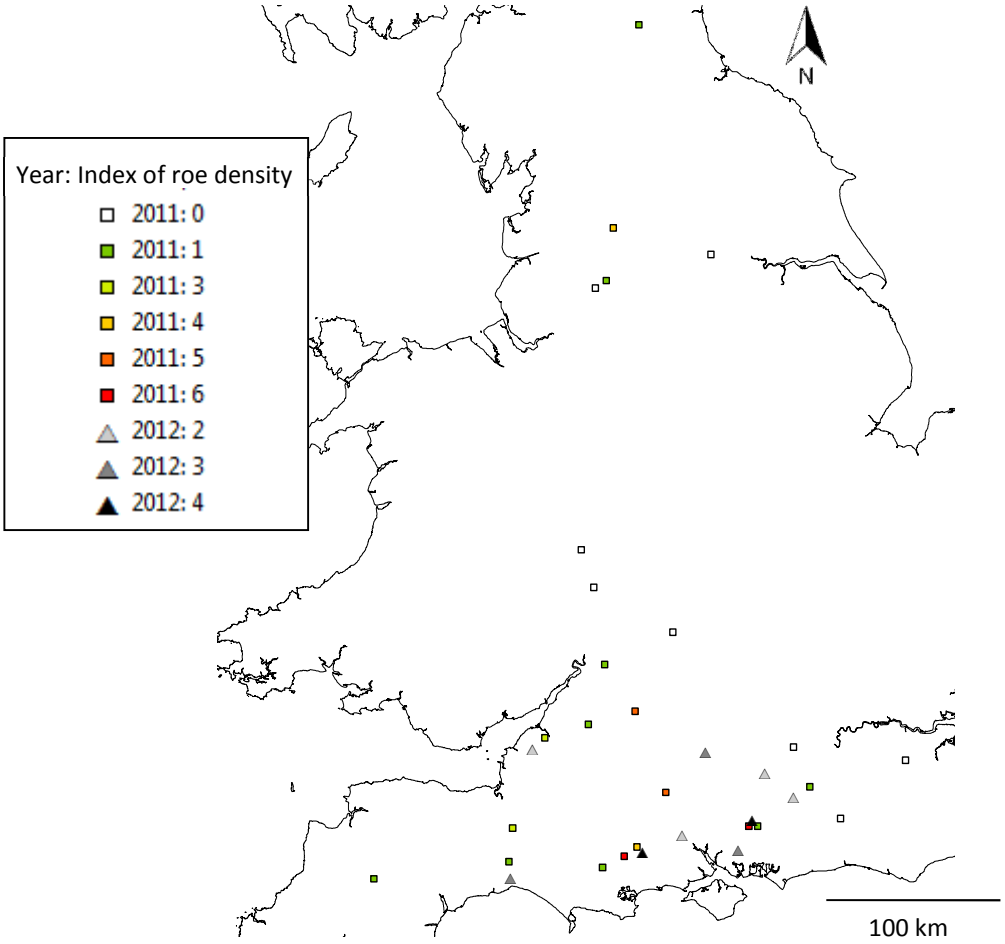


Figure 5-1. Location of field sites across England, visited during 2011 (squares) and 2012 (triangles). Different colours represent differing mean number of roe deer recorded by Breeding Bird Survey volunteers in each of the field sites.

Table 5-1. Pearson's correlation (R) between potential predictor variables used in later analyses. MTCO is the mean temperature of the coldest month and GDD5 is the number of growing degree days above 5°C. Climate data were obtained at a 1km^2 resolution (i.e. at the site scale) from the Met Office and soil fertility data from the National Soil Resources Institute (see '*Site characteristics*' above).

Predictor variables	*R*	*t*	*d.f.*	*p*
MTCO, GDD5	0.84	8.88	34	0.001
MTCO, summer precipitation	-0.37	-2.35	34	0.02
MTCO, soil fertility	0.35	2.18	34	0.04
Soil fertility, GDD5	0.29	1.74	34	0.09
Soil fertility, summer precipitation	-0.26	-1.57	34	0.12
Summer precipitation, GDD5	-0.51	-3.50	34	0.001

5.3.4. Vegetation recording

Each of my vegetation data collection methods are described in detail below. However, in summary, vegetation data collected at each site included: quadrats to determine

ground flora- and shrub layer- species composition and percentage cover, photography to determine canopy cover, a 'point-centred quarter' method (Cottam et al. 1953) to obtain measures of tree density, aerial woody volume and species composition, and an adaptation of the profile board (Nudds 1977) to obtain measures of shrub layer density. Each of these collection methods are described below.

Recording tree species composition

At each of five randomly-selected plot locations within each 1km^2 site, the point-centred quarter method (Cottam et al. 1953) was used to estimate the structure and composition of large shrubs and trees (Smith and Smith 2001). Total tree density, total basal area per unit area of ground, and the frequency, density and basal area for each species were estimated. Centre points were located far enough away from each other that no tree was measured twice.

Estimating shrub layer density

Shrub layer density between 0 and 2m from the ground was estimated using an adaptation of the vegetation profile board developed by Nudds (1977). A 2x2m white sheet was erected at each of five randomly selected point locations within each 1km^2 site (Figure 5-2). At each point, two photographs of the sheet were taken (one from each side of the sheet) from 4m away using a digital camera, from a height of approximately 1m.

Figure 5-2. Photograph showing equipment layout for measuring vegetation density.

Photographs were analysed in the laboratory using *ImageJ*, an image processing and analysing program (Rasband 2010). Each image was cropped to show only the 2x2m sheet (plus any vegetation in front of it) and then converted to a black and white image; black areas represented vegetation cover (Figure 5-3). Areas of black and white image were calculated using the 'png' package in R (Urbanek 2012), and the proportion of vegetation cover calculated for each of the four, 50cm horizontal bands of the 2m high sheet.

Figure 5-3. Cropped photograph (A) converted to binary (B), ready for analysis.

Measuring species composition and abundance

Species composition and abundance were estimated using quadrats. Ground layer species richness and percentage cover of each plant species was recorded in two (2 x 2m) quadrats at each of five randomly-selected plot locations within each 1km^2 site. These plot locations coincided with the five locations where shrub layer density photographs were taken. 5 x 5m quadrats were used to estimate species composition of the shrub layer, in a similar way to measurement of the ground layer.

Species diversity for each layer was calculated using Simpson's Index of Diversity, D_S,

where: $$D_S = 1 - \sum \left(\frac{n_i}{N}\right)^2$$ ***Equation 5.2.***

Where n_i = the total number of species *i,*

and N = the number of individuals of all species.

Simpson's Index of Diversity ranges between 0 (low diversity) and 1 (high diversity).

Measuring canopy cover

Ten photographs of the canopy were taken per site i.e. two photographs at each of five randomly-selected plot locations within each 1km^2 site using a digital camera pointed upwards from head height. Photographs were converted to binary images using a threshold to differentiate sky and vegetation as white and black pixels respectively. The number of black and white pixels were calculated: black pixels represented vegetation, and white pixels the sky. The percentage cover of vegetation was calculated per image, and then the mean vegetation cover in the canopy was calculated per site. Canopy cover was used as a measure of sunlight availability which strongly influences understorey vegetation, for example by affecting assimilation rates and the growth of roots, shoots and leaves (Wilcox et al. 1981).

5.3.5. Data analyses

All data analysis was conducted using R (R Core Team 2013). Covariate predictors used in all models (described below) were: roe deer density (see page 100), soil fertility, GDD5, and canopy cover. Each of these values was calculated as the mean per site, as described in the '*site characteristics'* section. Survey year ('year') was also included as a fixed factor in all models, to account for potential inter-year differences. I fit multiple regression models [i.e. full models with all predictors (as per, for example, Gill and Fuller 2007, Scott et al. 2009)] via maximum likelihood, as all of the predictors were assumed to have a role in shaping vegetation characteristics.

Effects of deer on vegetation species' diversity and density

The relationships between species diversity of shrub and ground layers and shrub layer density were evaluated by fitting models with a beta error distribution and a logit link, using the 'betareg' package in R (Cribari-Neto and Zeileis 2010, Simas et al. 2010). I used beta regression as each of the response variables were values bounded by 0 and 1, but not binomial. Six models were fitted, one for each of the response variables: ground layer diversity, shrub layer diversity, and vegetation densities in each of the four height bands (band 1: 0 – 50cm from the ground; band 2: 50 – 100cm from the ground; band 3: 100 – 150cm from the ground; band 4: 150 – 200cm from the ground).

Effects of deer on vegetation cover

The relationships between cover (mean % cover per paired quadrat per site) of the shrub and ground layers, and the four predictors (roe density, soil fertility, GDD5 and canopy cover) were assessed by fitting generalised linear models with quasi-poisson error distributions and log links, given each of the over-dispersed response variables (abundance and cover of vegetation).

Effects of deer on vegetation abundance

Mann-Whitney U-tests (Mann and Whitney 1947) were used to compare the abundance (percentage cover in quadrats) of individual species in the ground and shrub layer of sites with and without roe deer. This non-parametric test was used because, even after transformation, data were zero-inflated and not normally distributed.

5.4. Results

A description of the characteristics of each site is provided in Table 5-2. The roe deer abundances in the subset of sites visited reflect the range of deer abundances recorded by the volunteers across all sites covered by the Breeding Bird Survey (BBS) (Figure 5-4); the mean number of roe deer seen during BBS at each field site ranged from 0 to 6, while across all BBS sites the range was from 0 to 17 roe deer. However, only five BBS sites across the whole of the U.K. had a higher mean roe density than 6. These sites lacked woodland cover and so were not visited as part of this study.

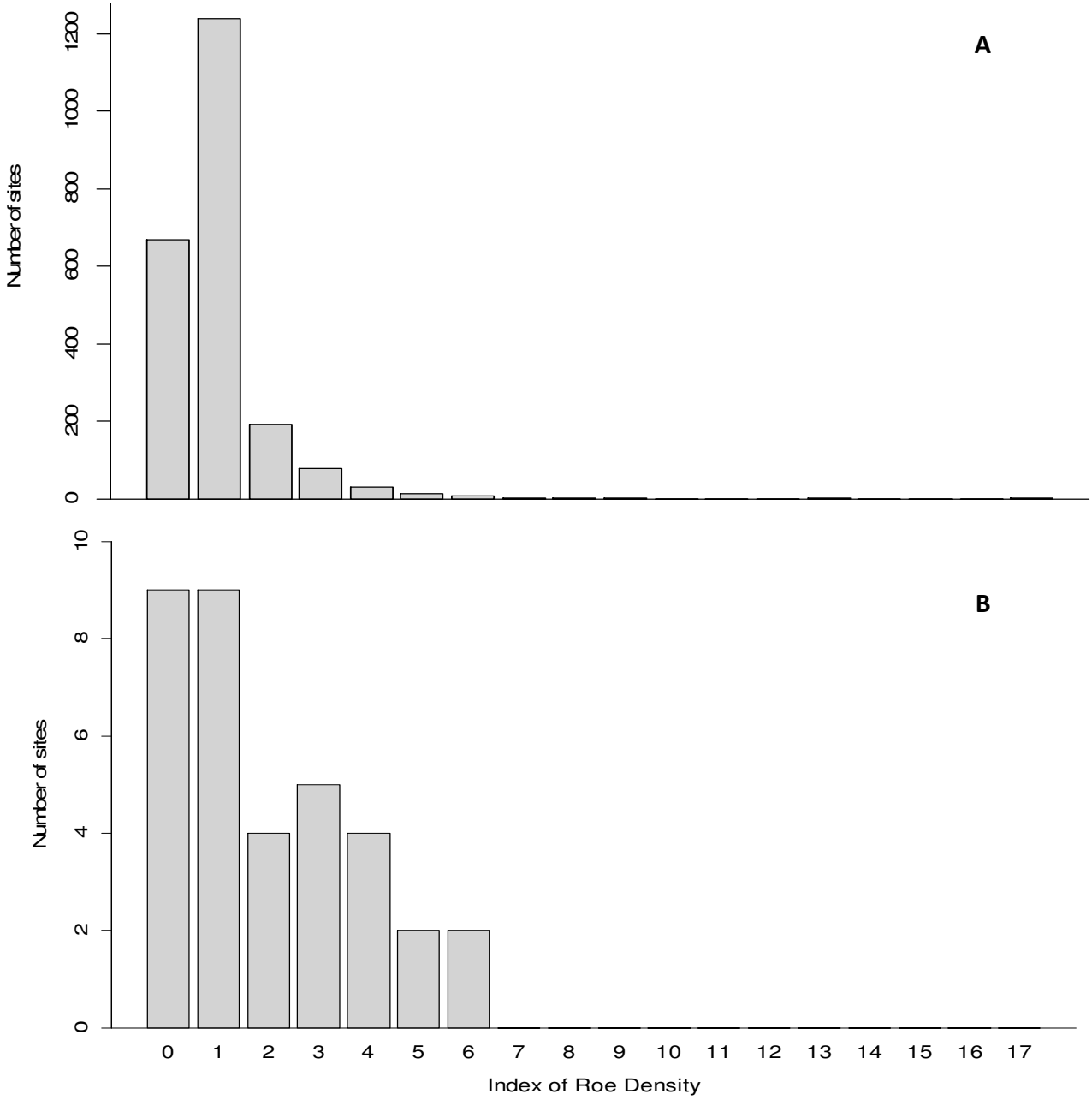


Figure 5-4. The mean number of roe deer recorded in each Breeding Bird Survey site, where roe deer were the only species recorded (A), and in the subset of field sites (B).

Table 5-2. Details of field sites visited during 2011 and 2012. 'No. years' represents the number of years Breeding Bird Survey volunteers have been visiting a given site, and mean roe density represents the mean number of roe deer recorded across the number of years the sites has been visited. 'GDD5' is the mean growing degree days over 5^{o}C per site over the years 1986 – 2006. Soil fertility ranges from 1 (low fertility) to 5 (high fertility). 'Canopy cover' represents the percentage cover of vegetation in the canopy per site, calculated using data from photographs of the canopy. Table continued on the next page.

BBS Ref.	Grid Ref.	Easting	Northing	No. Years	Mean roe density	Soil fertility	Canopy cover	GDD5	Year visited
620	SD8211	382000	411000	15	0.00	2	91	1503	2011
671	SE4629	446000	429000	10	0.00	3	92	1813	2011
814	SO7472	374000	272000	14	0.00	3	91	1795	2011
819	SO8152	381000	252000	15	0.00	3.33	91	2032	2011
886	SP2528	425000	228000	4	0.00	3	88	1841	2011
1470	SU9267	492000	167000	10	0.00	1	85	2061	2011
1503	SX2453	224000	53000	5	0.00	2	91	2011	2011
1987	TQ1829	518000	129000	5	0.00	2	93	2052	2011
2060	TQ5460	554000	160000	15	0.00	3.5	91	1927	2011
1943	TQ0146	501000	146000	15	0.57	2	84	1954	2011
822	SO8711	387000	211000	4	0.75	3	93	1978	2011
1157	ST7879	378000	179000	14	0.77	5	77	1846	2011
1516	SX5997	259000	97000	11	0.80	2	80	1783	2011
628	SD8815	388000	415000	14	0.83	2	87	1503	2011
1044	ST3406	334000	106000	4	1.25	3	85	1907	2011
1410	SU7225	472000	125000	4	1.25	2.5	85	1943	2011
523	NZ0651	406000	551000	9	1.38	2	73	1411	2011
1180	ST8603	386000	103000	10	1.44	3	80	1938	2011
1469	SU9240	492000	140000	16	1.64	1	47	1998	2012
1069	ST4766	347000	166000	12	1.90	5	86	2085	2012
1420	SU7653	476000	153000	15	2.14	3	90	2032	2012
1263	SU3020	430000	120000	16	2.20	3	83	2013	2012
1047	ST3624	336000	124000	3	3.00	4.5	88	2083	2011
1300	SU4364	443000	164000	4	3.00	3	92	1930	2012
1550	SY3597	335000	97000	10	3.00	1.5	93	1936	2012
1369	SU6112	461000	112000	13	3.15	3	77	2023	2012

BBS Ref.	Grid Ref.	Easting	Northing	No. Years	Mean roe density	Soil fertility	Canopy cover	GDD5	Year visited
1084	ST5472	354000	172000	12	3.17	5	91	2089	2011
1224	SU0811	408000	111000	14	3.54	3	63	1934	2012
1402	SU6928	469000	128000	4	4.00	2	91	1924	2012
634	SD9243	392000	443000	15	4.14	2	72	1443	2011
1217	SU0514	405000	114000	15	4.21	5	80	1934	2011
1216	SU0486	404000	186000	12	4.75	3	78	1920	2011
1244	SU2143	421000	143000	9	5.33	3	91	1929	2011
1203	ST9809	398000	109000	13	5.92	2.5	85	2022	2011
1396	SU6725	467000	125000	3	6.00	2	92	1924	2011

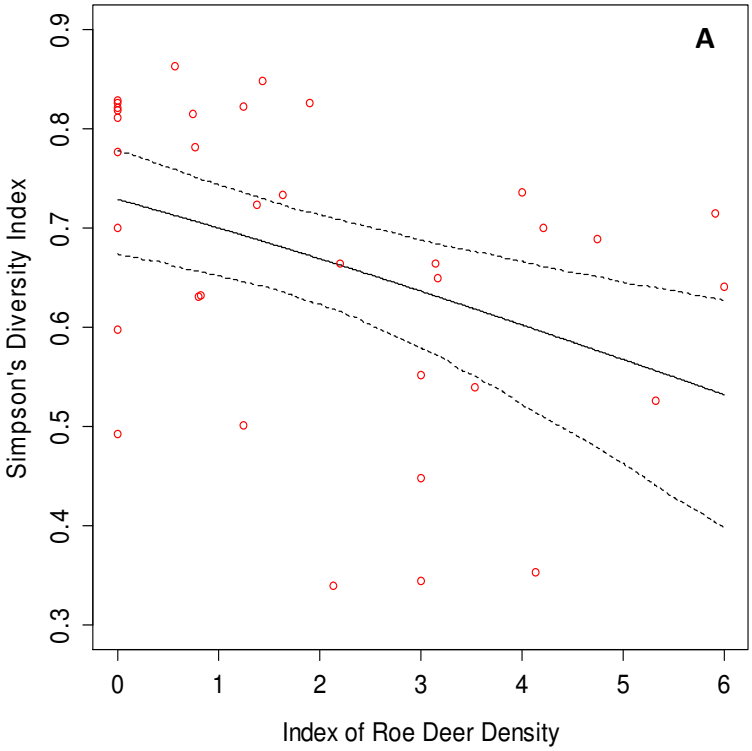
5.4.1. Effects of deer on vegetation diversity

Shrub layer diversity was negatively related to roe density (Z = -2.51, p < 0.01; Table 5-3, Figure 5-5). The data provided no support for a nonlinear relationship between shrub layer diversity and roe density as re-fitting the model with the addition of a quadratic term for roe density was not statistically significant (Z = 1.62, p = 0.11). Throughout this results chapter, all results were supported by the outcomes of model selection using AIC.

Ground layer vegetation diversity at the site level was negatively related to soil fertility (Z = -2.41, p < 0.02; Table 5-3). There was also a significant year effect, with higher ground layer diversity being recorded in sites surveyed in 2012 (n = 9) than those surveyed in 2011 (n = 26) (Z = 2.70, p = 0.01).

Table 5-3. Parameter values for beta regression models with beta error distributions and log link, for predicting ground and shrub layer diversity. Roe is the mean number of roe deer recorded by Breeding Bird Survey volunteers across all years' survey, per site. 'GDD5' is the mean growing degree days over 5^{o}C per site over the years 1986 – 2006. Soil fertility ranges from 1 (low fertility) to 5 (high fertility). 2011 is the reference year. 'Canopy cover' represents the percentage cover of vegetation in the canopy per site, calculated using data from photographs of the canopy. p denotes the significance of the Z-tests.

Model response	Parameter	Coef.	Z	p
Ground diversity	Intercept	2.45	2.37	0.02
	Roe	0.03	0.75	0.45
	Soil	-0.18	-2.41	0.02
	Canopy	0.003	0.31	0.76
	GDD5	-0.001	-1.06	0.29
	Year	0.56	2.70	0.01
Shrub diversity	Intercept	0.48	0.39	0.70
	Roe	-0.13	-2.51	0.01
	Soil	-0.02	-0.22	0.82
	Canopy	-0.01	-0.82	0.41
	GDD5	0.001	1.19	0.24
	Year	-0.41	-1.69	0.09



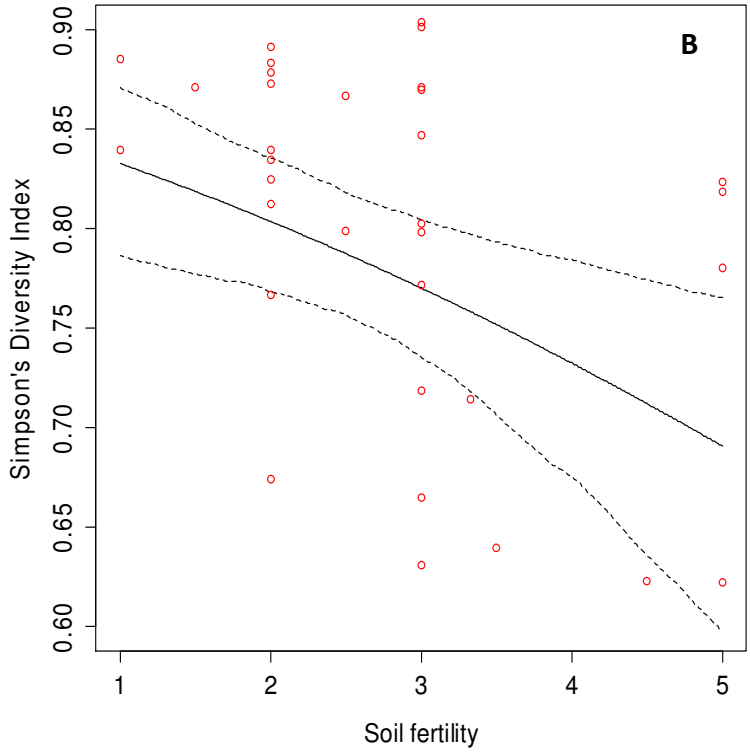


Figure 5-5. Variation in diversity of the shrub layer as function of roe deer density (A), and diversity of the ground layer a function of soil fertility (B). The solid lines represent the mean predicted values from 1000 bootstrapped replicates; dashed lines represent 95% confidence intervals of the predictions. Observed values are represented by red circles.

5.4.2. Effects of deer on tree sapling and tree seedling diversity

Diversity of trees in the shrub layer decreased with increasing deer density (Z = -2.42, p < 0.02; Table 5-4; Figure 5-6). Tree seedling diversity was negatively related to soil fertility (Z = -3.54, p < 0.01; Table 5-4).

Table 5-4. Parameter values for beta regression models with beta error distributions and log link, for predicting (Simpson's) diversity of saplings in the shrub layer, seedlings in the ground layer, and trees in the canopy. A description of predictors is provided in Table 5-3.

Model response	Parameter	Coef.	*Z*	*p*
Tree sapling diversity (shrub layer)	Intercept	0.44	0.34	0.73
	Roe	-0.13	-2.42	0.02
	Soil	-0.09	-0.88	0.38
	Canopy	-0.002	-0.17	0.87
	GDD5	0.0005	0.72	0.47
	Year	-0.33	-1.34	0.18
Tree seedling diversity (ground layer)	Intercept	-2.00	-0.72	0.47
	Roe	0.08	0.65	0.52
	Soil	-0.72	-3.30	0.01
	Canopy	-0.01	-0.38	0.71
	GDD5	0.002	1.74	0.08
	Year	-0.50	-0.92	0.36
Tree diversity (canopy layer)	Intercept	-0.70	-0.68	0.50
	Roe	-0.07	-1.24	0.21
	Soil	0.02	0.19	0.85
	GDD5	0.001	1.42	0.16
	Year	-0.15	-0.66	0.51

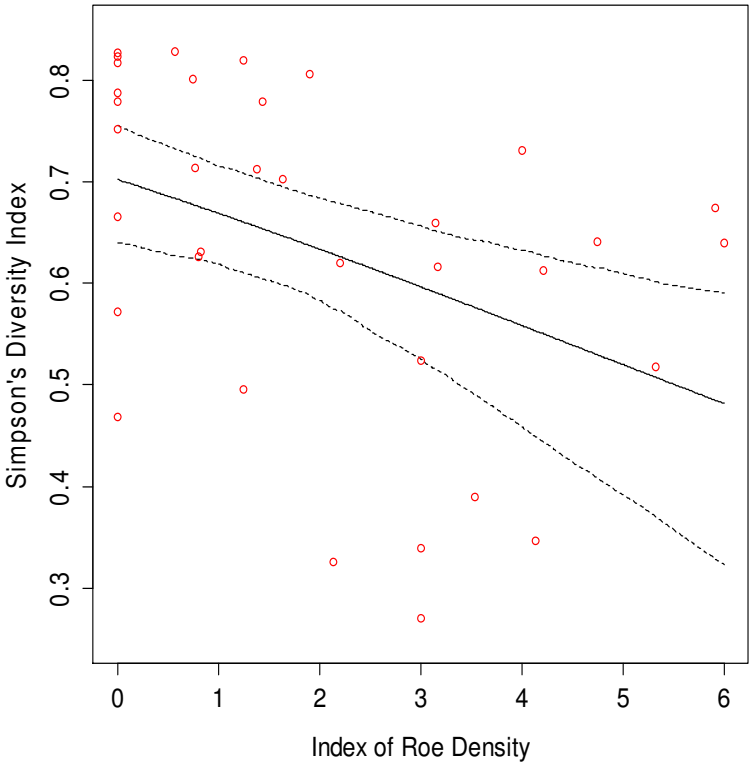


Figure 5-6. Variation in the diversity of trees in the shrub layer with roe deer density. The solid lines represent the mean predicted values from 1000 bootstrapped replicates; dashed lines represent 95% confidence intervals of the predictions. Observed values are represented by red circles.

5.4.3. Effects of deer on vegetation density

Vegetation cover was highest below 50cm from the ground; the mean proportion of vegetation cover across all paired shrub-layer photographs in all sites for the band 0 – 50 cm from the ground was 0.32, while for the bands 50 – 100cm, 100 – 150cm, and 150 – 200cm from the ground, the means were: 0.11, 0.08 and 0.08 respectively.

There was no significant relationship between roe density and vegetation density at any height (Table 5-5; band1: Z = -0.85, p = 0.40, band 2: Z = -0.68, p = 0.50, band3: Z = -0.70, p = 0.49, band 4: Z = -0.72, p = 0.47).

Table 5-5. Parameter values (on the logit scale) for the models predicting vegetation density in four bands: 0 – 50cm from the ground (band 1), 50 – 100cm from the ground (band 2), 100 – 150cm from the ground (band 3) and 150 – 200cm from the ground (band 4). A description of predictors is provided in Table 5-3.

Vegetation band	Parameter	Estimate	Std. Error	*Z*	*p*
1	Intercept	0.00	1.31	0.00	1.00
	Roe	-0.05	0.06	-0.85	0.40
	Soil	0.01	0.10	0.15	0.88
	GDD5	0.00	0.00	0.06	0.95
	Canopy	-0.01	0.01	-0.72	0.47
	Year	-0.43	0.27	-1.60	0.11
2	Intercept	-4.01	1.57	-2.55	0.01
	Roe	-0.04	0.06	-0.68	0.50
	Soil	-0.13	0.12	-1.10	0.27
	GDD5	0.00	0.00	0.91	0.36
	Canopy	0.01	0.01	1.02	0.31
	Year	-0.27	0.30	-0.91	0.36
3	Intercept	-6.26	1.81	-3.45	0.00
	Roe	-0.05	0.07	-0.70	0.49
	Soil	-0.07	0.13	-0.50	0.61
	GDD5	0.00	0.00	0.26	0.80
	Canopy	0.04	0.02	2.65	0.01
	Year	-0.06	0.32	-0.17	0.86
4	Intercept	-4.72	1.84	-2.57	0.01
	Roe	-0.05	0.08	-0.72	0.47
	Soil	-0.03	0.13	-0.24	0.81
	GDD5	0.00	0.00	0.59	0.55
	Canopy	0.02	0.02	1.08	0.28
	Year	-0.16	0.34	-0.46	0.65

5.4.4. Effects of deer on vegetation abundance

Shrub cover decreased linearly with increasing deer density (Table 5-6; $F_{1,33} = 6.67$, $p < 0.05$). Adding a quadratic term for roe density had no effect on model fit ($F_{1,32} = 0.00$, $p = 0.99$). Mean shrub cover decreased from 49% in sites with no deer to 32% in sites with the highest density of roe deer.

Table 5-6. Parameter values for generalised linear models for predicting ground and shrub layer cover. A description of predictors is provided in Table 5-3.

Model response	Parameter	Coef.	*d.f.*	*F*	*p*
Ground cover (%)	Intercept	5.90			
	Roe	-0.001	1,33	0.14	0.71
	Soil	0.11	1,32	1.55	0.22
	Canopy	-0.004	1,31	1.50	0.23
	GDD5	-0.001	1,30	5.38	0.03
	Year	0.18	1,29	2.16	0.15
Shrub cover (%)	Intercept	3.97			
	Roe	-0.05	1,33	6.67	0.02
	Soil	-0.04	1,32	0.67	0.42
	Canopy	0.003	1,31	0.55	0.46
	GDD5	-0.0001	1,30	0.34	0.57
	Year	-0.09	1,29	0.53	0.47

While there was no evidence of a significant relationship between roe deer density and ground layer cover ($F_{1,33} = 0.14$, $p = 0.71$; Table 5-6), there was a very weak negative relationship between ground layer percentage cover and GDD5 ($F_{1,30} = 5.38$, $p = 0.03$; Table 5-6). Mean ground layer cover was modelled to decrease from 110% [as vegetation is layered, cover can sum to over 100% (Sutherland 2006)] in sites with the lowest GDD5, to 80% in sites with the highest GDD5 (Figure 5-7b).

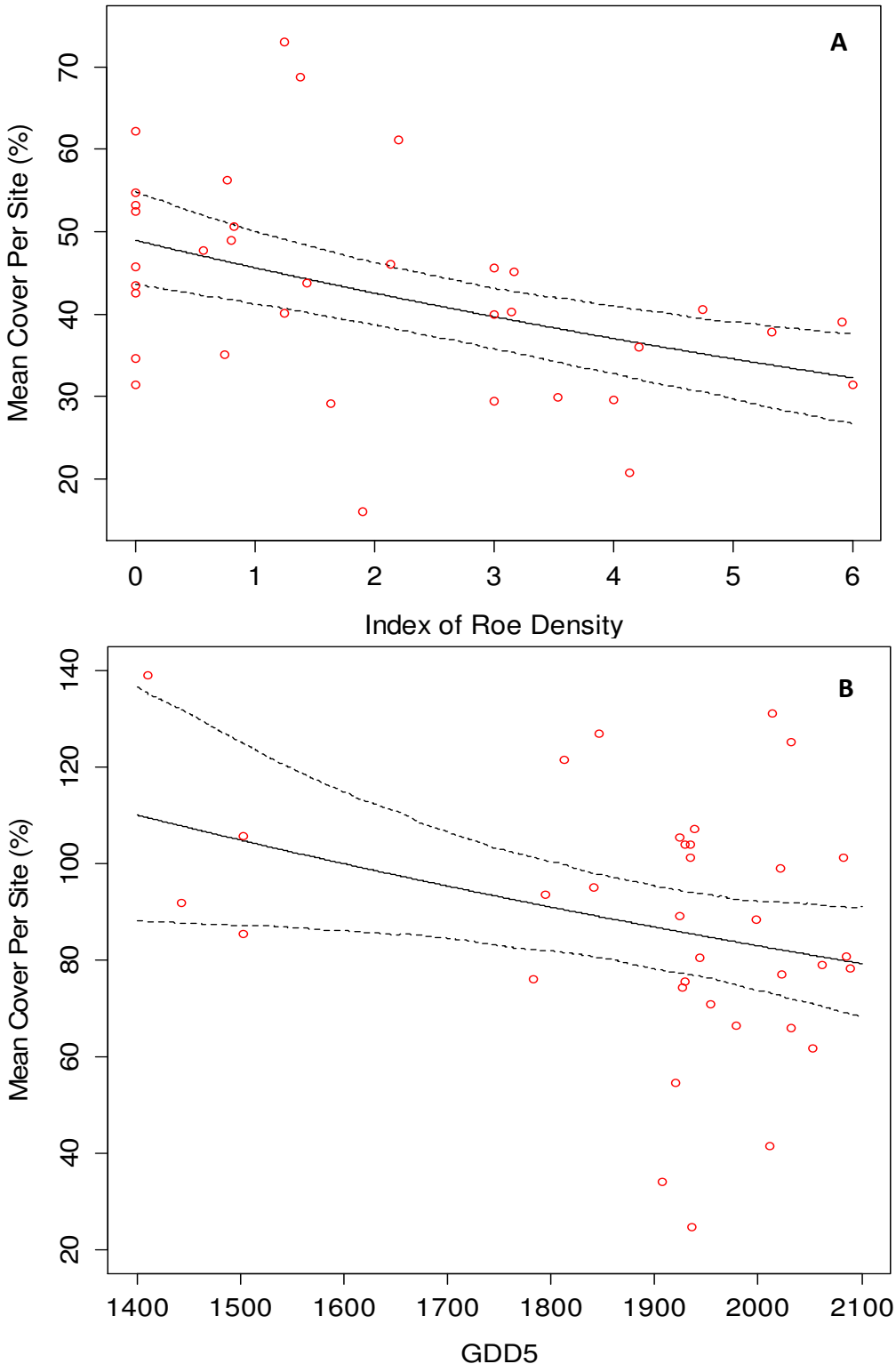


Figure 5-7. Variation in the proportion of overall shrub layer percentage cover in relation to deer density (A), and variation in overall ground layer percentage cover in relation to GDD5 (B). The solid lines represent the mean predicted values from 1000 bootstrapped replicates; dashed lines represent 95% confidence intervals of the predictions. Observed values are represented by red circles.

5.4.5. Effects of deer on vegetation abundance: individual species responses

The median percentage cover of elder in the shrub layer was significantly higher in sites without deer (2.3% in sites without deer versus 0.05% in sites with deer: $U_{9,26}$ = 59, $|Z|$ = 2.19, $p < 0.05$). Unsurprisingly, given the very high variability in the individual species data, no significant differences between the abundance of any of the other species recorded in either the shrub or the ground layers of sites with or without deer were found.

5.5. Discussion

Negative relationships were observed between roe deer density and the diversity and abundance of shrub-layer vegetation in woodlands sampled across England. The directions of these relationships are in agreement with similar studies investigating the impacts of deer on vegetation in Britain (Putman et al. 1989, Fuller 2001, Gill and Beardall 2001, Joys et al. 2004, Sage et al. 2004, Gill and Fuller 2007, Gill and Morgan 2010). However, to my knowledge, this is the first study in British woodlands looking solely at the impacts of one (small-bodied) deer species – the roe deer, without the use of exclosures, across a range of natural deer densities, and across a large number of sites.

The negative relationships observed between roe deer density and shrub-layer species' diversity and cover could potentially have wide-ranging implications for species dependent on that habitat for food, cover or for nesting and egg-laying opportunities. Indeed, other authors have attributed reductions in bird (Fuller 2001, Allombert et al. 2005a, Gill and Fuller 2007), mammal (Flowerdew and Ellwood 2001), and invertebrate (Baines et al. 1994, Pollard and Cooke 1994, Allombert et al. 2005b) diversity and abundance to reductions in vegetation structure and diversity caused by deer. Although not directly studied here, in woodlands with high deer densities, changes in shrub layer vegetation could also lead to changes in canopy composition (Husheer et al. 2003). If this were the case, the density of canopy birds would also be expected to decline in the longer-term, given that the density and species richness of birds increases as structural diversity and tree diversity increases (Gill 2000). The next

chapter will investigate the relationships between deer abundance and the abundance of birds dependent on shrub-layer vegetation.

The abundance of elder was significantly higher in sites without deer than in sites where roe deer were present. Elder is known to be palatable to deer (Bobek et al. 1979, Kay 1993), and is also an important food source for birds such as the bullfinch *Pyrrhula pyrrhula*, blue tit *Cyanistes caeruleus*, starling *Sturnus vulgaris*, song thrush *Turdus philomelos*, blackbird *Turdus merula*, blackcap *Sylvia atricapilla* and robin *Erithacus rubecula* (Atkinson and Atkinson 2002). No other significant relationships between the abundance of individual plant species and the density of deer were found. This is, in part, due to the high variability and small sample size of the data collected during the field surveys. However, other studies which have reported the same finding attributed it to density-dependent herbivory: in high density areas (roe) deer may intensely browse palatable species before moving on to new areas, giving the palatable species in the first area the chance to recover (Morecroft et al. 2001).

Studies using labour intensive methods to estimate deer density (such as thermal imaging surveys and pellet counts) in woodlands across the U.K. have produced estimates of maximum density in woodlands of circa 25 roe deer km^{-2} (J. Latham pers comm. in Harris et al. 1995, Gill et al. 1997, Ward 2001). The maximum count of roe deer in my field sites, obtained during line transects as part of the BBS, was 6 deer km^{-2}. However, this is undoubtedly an underestimate of actual density, given that roe deer are difficult to detect in woodland (Newson et al. 2012). By the same token, I have no reason to expect that the counts of deer recorded in BBS sites do not encompass the vast majority of natural variation in roe densities in woodlands across Britain given that the 3200 BBS squares surveyed annually are chosen randomly, and only 6 had mean roe deer counts higher than those included in this analysis (Figure 5-4). Furthermore, the BBS deer count data have been shown to correlate well with deer density estimates collected using more labour-intensive methods (Newson et al. 2012).

As the relationships I observed between roe deer density and the diversity and abundance of shrub layer vegetation were linear, I was unable to determine a threshold of deer density above which vegetation diversity and abundance declined,

and below which vegetation diversity and abundance increased. Besides, it may not be advisable to suggest a single threshold density anyway, as 'acceptable' damage levels will vary according to local conditions and conservation priorities (see Putman et al. 2011a for a review). As Putman *et al.* (2011a) state: "*simplistically, if there are no deer in an area...damage [from deer] cannot occur, while if there are many deer in any area, damaging impacts are more likely*". However, despite the linear relationship between deer density and shrub layer cover and diversity, it is unlikely that simply by reducing deer density, vegetation cover and diversity will increase. Indeed, empirical (Tanentzap et al. 2009, Tanentzap et al. 2011, Nuttle et al. 2014) and theoretical studies (Tanentzap et al. 2013) have shown that a combined approach of reducing deer density, re-planting trees, and removal of ferns is required to encourage vegetation regeneration.

Similar studies to those conducted here, focussing on other wild deer species, would be beneficial so that tailored management plans could be drawn up for woodlands with different (combinations of) deer species. Additionally, while I accounted for canopy shading in the models, an experimental design explicitly taking into account the age of woodlands would be beneficial, given the potentially different impacts deer may have in woodlands of different ages (see Joys et al. 2004). Historic deer management strategies have also been shown to influence vegetation structure and abundance for many decades (Nuttle et al. 2014). Despite not explicitly accounting for woodland age in my analyses, I found no relationships between canopy cover, (or soil fertility or GDD5) and the density, abundance or diversity of shrub layer vegetation. Similarly, there was no relationship between roe density and ground layer vegetation cover or diversity; ground layer cover was negatively related to GDD5, and ground layer diversity was negatively related to soil fertility. The negative relationship between GGD5 and ground layer cover is counter to expectation, but could be a result of having a low number of sites with low GGD5 values (Figure 5-7b).

Deer are an important part of ecosystems, with some browsing beneficial to the growth and regeneration of woodlands (Mayle 1999). However, I have shown that as deer density increases, the abundance and diversity of shrub layer vegetation decreases. It is expected that the range and abundances of (roe) deer are likely to

increase in the future (see Chapter 4), possibly to unprecedented levels (Fuller and Gill 2001, Ward 2005, Ward et al. 2008). If this happens, the impacts presented here may be amplified in the future. Accordingly, a combination of management approaches including thinning of trees (Gill and Fuller 2007), temporary protection from browsing using either tree guards or deer fencing, and increased deer culls (Fuller 2001), will be needed to balance maintaining biodiversity with deer welfare, as the ranges and abundances of deer increase. However, short-term control of herbivores has been shown to have effects which do not persist long-term. Therefore long-term management of herbivores is advocated for the regulation of their negative impacts, which include the reduction of vegetation cover and increased tree mortality as their abundances increase (Gormley et al. 2012). A combination of predictive species' distribution models (e.g. Chapter 4) and predictive browse models (e.g. Holland et al. 2013, Tanentzap et al. 2013) will be useful tools in aiding herbivore management: such models can be used to identify and prioritise locations where pre-emptive management may be required, and where management will be most beneficial. Furthermore, as mentioned previously, the impacts of herbivory on shrub layer vegetation is likely to have cascading effects on other taxa, such as birds, which rely either directly or indirectly on that habitat; in the next chapter I investigate this relationship.

Chapter 6 : Rapid changes in avian community structure driven by deer

6.1. Abstract

Background: In recent decades, the distribution and abundance of deer, a keystone species group in many temperate environments, have increased dramatically, and have been shown to impact on a wide range of species within the environments they inhabit. Here, I investigate whether the observed increases in deer populations in Britain have had an impact on the abundance of woodland birds.

Methodology: Using annual count data collected from 1811 woodland sites across Britain between 1994 and 2010, I created population trends for 31 woodland bird species, and three deer species. I contrasted the multi-species composite population trends of groups of deer-sensitive and deer-tolerant woodland birds, and related the divergence of these two trends – termed the Deer Impact Indicator – to the temporal trend for deer.

Findings: The composite population trends for deer-tolerant birds increased by 7% while deer-sensitive birds decreased by 9% over the same study period. The divergence in the two bird trends increased by 18% over the study period, and showed a strong positive correlation to the composite population trend for deer (after accounting for a lagged- year effect; $S_{30} = 0.92$, $p < 0.01$), which increased by 48%.

Conclusions: I have shown that changes in the abundance of woodland birds are strongly associated with preceding changes in the abundances of deer. My results demonstrate the potential for rapid and profound impacts as a consequence of the expansion of deer in Britain, and potentially more widely, as resurgent populations of herbivorous ungulates are occurring in many countries worldwide.

6.2. Introduction

Deer exert cascading effects on other components of biodiversity in ecosystems they inhabit (Fuller and Gill 2001, Côté et al. 2004, Ripple and Beschta 2012, White 2012). In order to manage deer populations effectively, there is a need to understand and quantify these impacts (Cumming et al. 1997, Rooney and Waller 2003, Côté et al. 2004, Ward 2005), especially as their populations are likely to continue to increase in the future (Chapter 4) (Côté et al. 2004, Hemami et al. 2005).

The populations of numerous woodland bird species in Britain have declined rapidly in the past few decades (Gregory et al. 2007, Hewson et al. 2007, Hewson and Noble 2009), and it has been suggested that increasing browsing pressure from deer has been proposed to be one of the key contributors to such declines (Vanhinsbergh et al. 2001, Fuller et al. 2005). This is supported by local-scale experimental studies, which have shown a relationship between an increase in deer abundance and a decrease in the abundance (Degraaf et al. 1991, McShea and Rappole 2000, Baiser et al. 2008) or diversity (Casey and Hein 1983) of birds. For example, in Britain roe, fallow and muntjac deer have been shown to reduce the abundance and diversity of shrub layer plants (Gill and Fuller 2007, Holt et al. 2010), resulting in cascading impacts on several bird species that are dependent on understorey vegetation for food, cover or nesting opportunities, such as the willow warbler *Phylloscopus trochilus*, nightingale *Luscinia megarhynchos*, song thrush *Turdus philomelos*, chiffchaff *Phylloscopus collybita* (but see http://www.bto.org/birdtrends2010/wcrchiff.shtml, accessed 20/08/13) and willow tit *Poecile montanus* (Gill and Fuller 2007, Holt et al. 2010, Newson et al. 2012). Such cascading effects of deer are becoming increasingly widespread and, accordingly, are best viewed as landscape scale, rather than local-scale events (Dolman et al. 2010, Newson et al. 2012).

In America and Europe, where extensive long-term avian monitoring schemes have been undertaken, species-specific and composite population trends of birds (Fewster et al. 2000, Freeman et al. 2007, Gregory et al. 2007, Hewson et al. 2007, Hewson and Noble 2009, DEFRA 2011, Chollet and Martin 2013) (and mammals: Newson and Noble 2006) have been calculated as a tool to demonstrate community-level changes in populations, including general declines in the abundances of woodland birds.

Community-level indices have also been used to create generalised indicators of environmental impacts on animal populations. For example, Gregory *et al.* (2009) created a 'Climate Impact Indicator', which measured the divergence of population trends of birds in two groups: those expected to be favourably affected by climate change and those expected to be adversely affected. Such indicators are easy to interpret and highly useful for describing general patterns of change in impacts over time, raising awareness of the environmental driver, and assisting in setting strategies to reduce – or mitigate against – negative impacts such as reduced species abundances (Gregory et al. 2009, Jiguet et al. 2012).

Despite evidence for the cascading effect of deer on birds (Zalba and Cozzani 2004, Allombert et al. 2005a), temporal trends in avian community abundance have not been directly related to temporal trends in deer abundance. Here, I address this deficit by comparing the composite population of deer in 1811 woodland sites across England, to the divergence in the population trends of two groups of woodland birds. I develop a generalised indicator of the impact of deer on bird communities – termed the 'Deer impact indicator' (DII) – using a long-running, randomised and high resolution dataset of both bird and mammal abundances in Britain. Specifically, I first produce individual population trends for birds and deer in woodland sites across Britain. Second, I calculate the composite population trends for deer and for two groups of birds, classed as either deer-sensitive or deer-tolerant based on their reliance on shrub-layer habitats. Third, I calculate the DII by calculating the divergence in composite population trends of deer-sensitive and deer-tolerant bird species. Finally, I explore the influence of deer and climate on bird population trends by correlating the pattern of change in the DII to the composite population trend for deer and to temporal changes in climate. I allowed for time-lags in these relationships given the expectation that changes in habitat structure by deer, and climate, will not affect bird populations immediately (Hewson and Noble 2009).

6.3. Methods

6.3.1. Data sources

I use count data collected as part of the British Trust for Ornithology's Breeding Bird Survey (BBS) monitoring scheme, which also records mammal species, between 1994 and 2011. Details of the BBS methodology are described in Chapter 2. These data were used to identify sites where I would expect deer to have an impact on birds associated with shrub-layer vegetation; I excluded sites with more than 25% urban or upland habitat, as well as those with more than 25% urban cover (from Land Cover Map 2000 data: www.ceh.ac.uk/AccessingLCMData.html) (following Newson et al. 2012). Consequently, data collected from 1811 predominantly woodland BBS sites (Figure S 1, page 172) were used in the analysis. BBS data for 2001 were excluded from all analyses given the reduction in recording as a result of a foot-and-mouth outbreak in that year (Newson and Noble 2006). I considered the impact of three deer species – fallow deer, roe deer and Chinese muntjac deer (following Newson et al. 2012) – on woodland birds; the other three British deer species (red, sika and CWD) were excluded as they have either have relatively localised distributions (Figure 1-2) or are poorly monitored by the BBS (Wright et al. in Newson et al. 2012).

Species classed as 'woodland birds' (based on DEFRA (2011), were split into two groups (those assumed to be 'deer-tolerant' (n = 16), or negatively affected by deer herbivory, hereafter termed 'deer-sensitive' (n = 15)) based upon their feeding and nesting habitat preferences (Table 6-1). The abundances of three species classed as woodland birds by DEFRA have been suggested to increase under increased deer density– wood warbler *Phylloscopus sibilatrix*, tree pipit *Anthus trivialis* and redstart *Phoenicurus phoenicurus* (Fuller 2001, Gill and Fuller 2007) – and so were excluded from the analyses. Hawfinch *Coccothraustes coccothraustes* was also excluded as there were insufficient data to calculate a population trend for this species.

Annual climate data at a 10km^2 resolution were obtained from UKCIP (www.ukcip.org.uk), for the years 1994 to 2006; data for 2007 onwards are not yet available. I calculated the mean growing degree days above 5°C (GDD5) and mean

temperature of the coldest month (MTCO) each year, across each of the 1811 BBS sites used in the analyses (Figure S 2, page 173).

Table 6-1. Foraging preferences and nesting locations of woodland bird species. Foraging and nesting locations are mainly taken from (A) Hewson & Noble (2009), but are augmented and supported by: (B) Vanhinsbergh *et al.* (2001) and (C*) Newson *et al.* (2012). An 'MB' in the migrant column signifies that species is a migrant breeder, taken from Robinson (2005).

	Species					
Group	Common name	Scientific name	Foraging location	Nesting location	Refs	Migrant
Deer-tolerant birds	Sparrowhawk	*Accipiter nisus*	Various	Tree	A	
	Long-tailed tit	*Aegithalos caudatus*	Trees	Variable	A	
	Siskin	*Carduelis spinus*	Trees	Tree	B	
	Treecreeper	*Certhia familiaris*	Trees	Cavity	A	
	Greater spotted woodpecker	*Dendrocopos major*	Trees	Cavity	A	
	Lesser spotted woodpecker	*Dendrocopos minor*	Trees	Cavity	A	
	Chaffinch	*Fringilla coelebs*	Various	Tree	A; C	
	Jay	*Garrulus glandarius*	Ground	Tree	A	
	Spotted flycatcher	*Muscicapa striata*	Trees	Cavity	A	
	Coal tit	*Parus ater*	Trees	Cavity	A	
	Blue tit	*Parus caeruleus*	Trees	Cavity	A; C	
	Great tit	*Parus major*	Various	Cavity	A	
	Green woodpecker	*Picus viridis*	Ground	Cavity	A	
	Goldcrest	*Regulus regulus*	Trees	Tree	A	
	Nuthatch	*Sitta europaea*	Trees	Cavity	A; C	
	Tawny owl	*Strix aluco*	Ground	Cavity	A	
Deer-sensitive birds	Lesser redpoll	*Carduelis cabaret*	Trees	Understorey	A	
	Robin	*Erithacus rubecula*	Ground	Ground	A; C*	
	Nightingale	*Luscinia megarhynchos*	Ground	Understorey	A; B; C	MB
	Willow tit	*Parus montanus*	Various	Cavity	A; B; C	
	Marsh tit	*Parus palustris*	Various	Cavity, tree roots, ground	A; B; C	
	Chiffchaff	*Phylloscopus collybita*	Trees	Understorey	A; C	MB
	Willow warbler	*Phylloscopus trochilus*	Understorey	Ground	A; B; C	MB
	Dunnock	*Prunella modularis*	Ground	Understorey	A; B; C	
	Bullfinch	*Pyrrhula pyrrhula*	Various	Understorey	A; B; C	
	Blackcap	*Sylvia atricapilla*	Various	Understorey	A; C	MB
	Garden warbler	*Sylvia borin*	Various	Understorey	A	MB
	Lesser whitethroat	*Sylvia curruca*	Understorey	Understorey	A	MB
	Wren	*Troglodytes troglodytes*	Understorey	Understorey	A	
	Blackbird	*Turdus merula*	Ground	Understorey	A; C	
	Song thrush	*Turdus philomelos*	Ground	Understorey	A; B; C	

* Newson *et al.* (2012) class the robin *Erithacus rubecula* as a 'control species', not expected to be affected by deer. However, we include this species as a 'deer-sensitive' species given its feeding and nesting behaviour.

6.3.2. Calculation of species-specific population trends

Population trends for each bird and deer species were obtained by fitting generalised linear models to count data using a log link function, assuming a poisson- (birds, roe deer and muntjac deer) or negative binomial- (for fallow deer) distribution and accounting for over-dispersion. Negative binomial error distributions were chosen for the fallow deer models to reduce the influence of herding behaviour of this species during model fitting (following Newson and Noble 2006). Smoothed population trends for each species were then calculated by fitting generalised additive models (GAMs) to annual indices, using a smoothed year effect with 5 degrees of freedom (Fewster et al. 2000). Smoothed species-specific population trends were calculated this way due to the difficulty of fitting GAMs directly to the bird census data (www.bto.org/about-birds/birdtrends/2011/methods/statistical-methods-alerts, accessed 25th February 2012). Smooth trends were used as they reduce (or remove, depending on the number of degrees of freedom) between-year fluctuations in population sizes, while retaining the major features of the trend (Hewson and Noble 2009). The initial value of the trend was set to 100 in 1994 for birds and 1995 for deer (as deer data were collected as part of the BBS from 1995 onwards). Annual trends for all years to 2011 were rescaled relative to the population size in the reference year. When calculating changes in trend, the start and end years were truncated to ensure end effects (due to the use of GAMs) did not bias inference (Fewster et al. 2000).

6.3.3. Calculation of composite population indices and the Deer Impact Indicator (DII)

For the deer-sensitive and deer-tolerant bird groups as well as for deer, I calculated composite population indices; for each year from 1994 (1995 for deer) to 2011, the log of each species' population trend was taken, averaged across all species in the group, and then the exponent of the result obtained. A geometric mean was used so that a doubling of the index from 100 to 200 was equivalent, but opposite, to a decline in index from 100 to 50 (Gregory and van Strien 2010). 90% confidence intervals for the composite deer population trend were calculated following two steps. Firstly, for each deer species in turn, sites were randomly re-sampled (with replacement) and annual

trends re-calculated using GLM and GAMs (as above). The composite trend across each of the 10,000 bootstrapped replicates was then calculated.

For a given year, the DII was calculated as the ratio of the composite population index for deer-tolerant to that of deer-sensitive bird species. 90% bootstrap confidence intervals for annual values, from 10,000 bootstrapped replicates (re-sampling birds with replacement), were obtained using the methodology described by Gregory *et al.* (2009).

6.3.4. Correlations between DII change and changes in deer and climate trends

Spearman's rank correlations (as data were not normally distributed) between the DII and GDD5, MTCO and the composite deer population trend were calculated with lags of between 0 and 3 years between change in the driver and change in the DII. I explored time lags due to the expectation that deer and climate would not affect bird populations immediately (Hewson and Noble 2009). It was expected that impacts of climate and deer would occur indirectly through impacts on vegetation (Newson et al. 2012), and directly through effects on, for example, egg-laying behaviour (Crick et al. 1997) and survival (Robinson et al. 2007).

6.4. Results

6.4.1. Species-specific population trends

Nine of the deer-tolerant bird species increased significantly between 1995 and 2010, while four species declined significantly (Table 6-2). Conversely, seven of the deer-sensitive species declined significantly over the study period, and six increased significantly (Table 6-2). The most dramatic increase in population size was observed for the great spotted woodpecker *Dendrocopos major* (+121%), and the most dramatic decrease was observed for the willow tit *Parus montanus* (-72%).

The population trends of roe and muntjac deer increased significantly over the study period (Figure 6-1, Table 6-2). The population trend for fallow deer also increased over the study period, though this trend was non-significant (Table 6-2).

Table 6-2. Percentage change in population trends for woodland birds and deer between 1995 and 2010 (birds) and 1996 and 2010 (deer). When the upper (UCL) and lower (LCL) confidence limits of the trend in 2010 do not overlap with 100, this indicates a significant change in population size for a species between the first and last years (marked with an asterisk (*) in the 'sig' column).

	Species					
Group	Common name	Scientific name	Change	Sig.	LCL	UCL
Deer-tolerant birds	Sparrowhawk	*Accipiter nisus*	-16	*	73	85
	Long-tailed tit	*Aegithalos caudatus*	10		96	116
	Siskin	*Carduelis spinus*	58	*	154	198
	Treecreeper	*Certhia familiaris*	-9		81	109
	Greater spotted woodpecker	*Dendrocopos major*	121	*	225	237
	Lesser spotted woodpecker	*Dendrocopos minor*	-30	*	43	75
	Chaffinch	*Fringilla coelebs*	6	*	103	111
	Jay	*Garrulus glandarius*	2	*	86	98
	Spotted flycatcher	*Muscicapa striata*	-44	*	39	55
	Coal tit	*Parus ater*	20	*	115	131
	Blue tit	*Parus caeruleus*	9	*	107	119
	Great tit	*Parus major*	36	*	132	144
	Green woodpecker	*Picus viridis*	43	*	135	155
	Goldcrest	*Regulus regulus*	6		90	138
	Nuthatch	*Sitta europaea*	71	*	162	182
	Tawny owl	*Strix aluco*	-26	*	53	81
Deer-sensitive birds	Lesser redpoll	*Carduelis cabaret*	-12		38	140
	Robin	*Erithacus rubecula*	9	*	103	115
	Nightingale	*Luscinia megarhynchos*	-39	*	36	60
	Willow tit	*Parus montanus*	-72	*	7	27
	Marsh tit	*Parus palustris*	-25	*	62	82
	Chiffchaff	*Phylloscopus collybita*	56	*	138	178
	Willow warbler	*Phylloscopus trochilus*	-24	*	76	84
	Dunnock	*Prunella modularis*	15	*	107	119
	Bullfinch	*Pyrrhula pyrrhula*	-8	*	77	97
	Blackcap	*Sylvia atricapilla*	88	*	181	201
	Garden warbler	*Sylvia borin*	-11		84	96
	Lesser whitethroat	*Sylvia curruca*	6		81	101
	Wren	*Troglodytes troglodytes*	-6	*	75	99
	Blackbird	*Turdus merula*	20	*	117	125
	Song thrush	*Turdus philomelos*	23	*	113	129
Deer	Roe	*Capreolus capreolus*	54	*	147	162
	Fallow	*Dama dama*	25		91	136
	Muntjac	*Muntiacus reevesi*	64	*	144	184

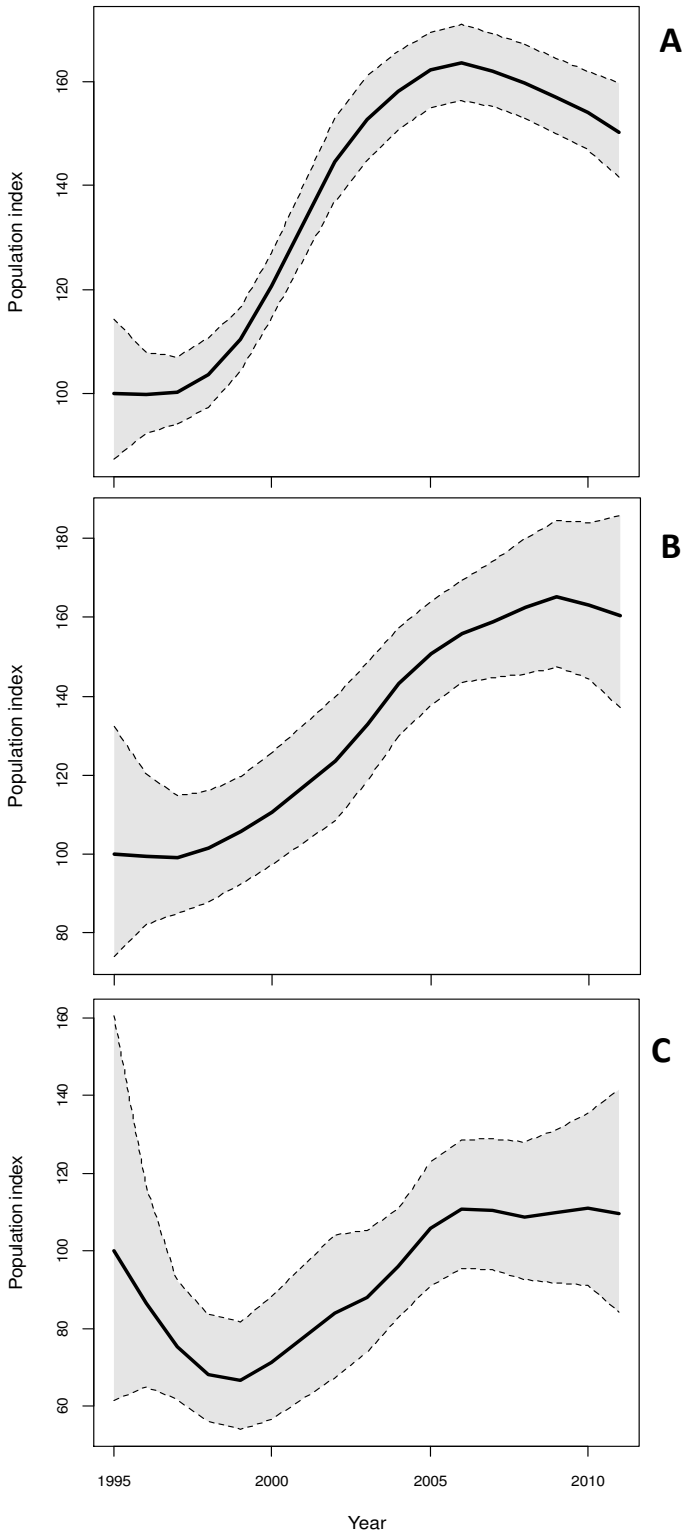


Figure 6-1. Population trend for (A) roe deer, (B) muntjac deer, and (C) fallow deer. The bold lines show the geometric mean of the individual species population trends. Anything above an index of 100 represents an increase in the index relative to the start year, and vice versa. The shaded polygons represent the 90% bootstrap confidence intervals for annual values, from 10,000 bootstrapped replicates (Gregory et al. 2009).

6.4.2. Composite population indices

Overall, populations of deer-tolerant bird species (*n* = 16) increased by 7% between 1995 and 2010, while populations of deer-sensitive bird species (*n* = 15) declined by 9% over the same time period (Figure 6-2). The composite population trend for deer increased by 48% between 1996 and 2010 (Figure 6-2); the most pronounced changes in this trend occurred between 1998 and 2006.

6.4.3. The Deer Impact Indicator (DII)

The DII, which reflects the divergence in composite population indices of groups of birds, depending on whether they are expected to be negatively impacted by deer or not, increased by 18% between 1995 and 2010 (Figure 6-3). The most pronounced increase occurred between 2000 and 2007.

6.4.4. Correlations between DII change, deer trend and climate trends

The DII showed a very strong positive correlation with the composite population trend of deer (Figure 6-4). This correlation was strongest when it incorporated a one-year time lag between a change in deer abundance and a change in the DII (Table 6-3). No significant correlations between the DII and climate were found, even after accounting for potential time lags (Table 6-3).

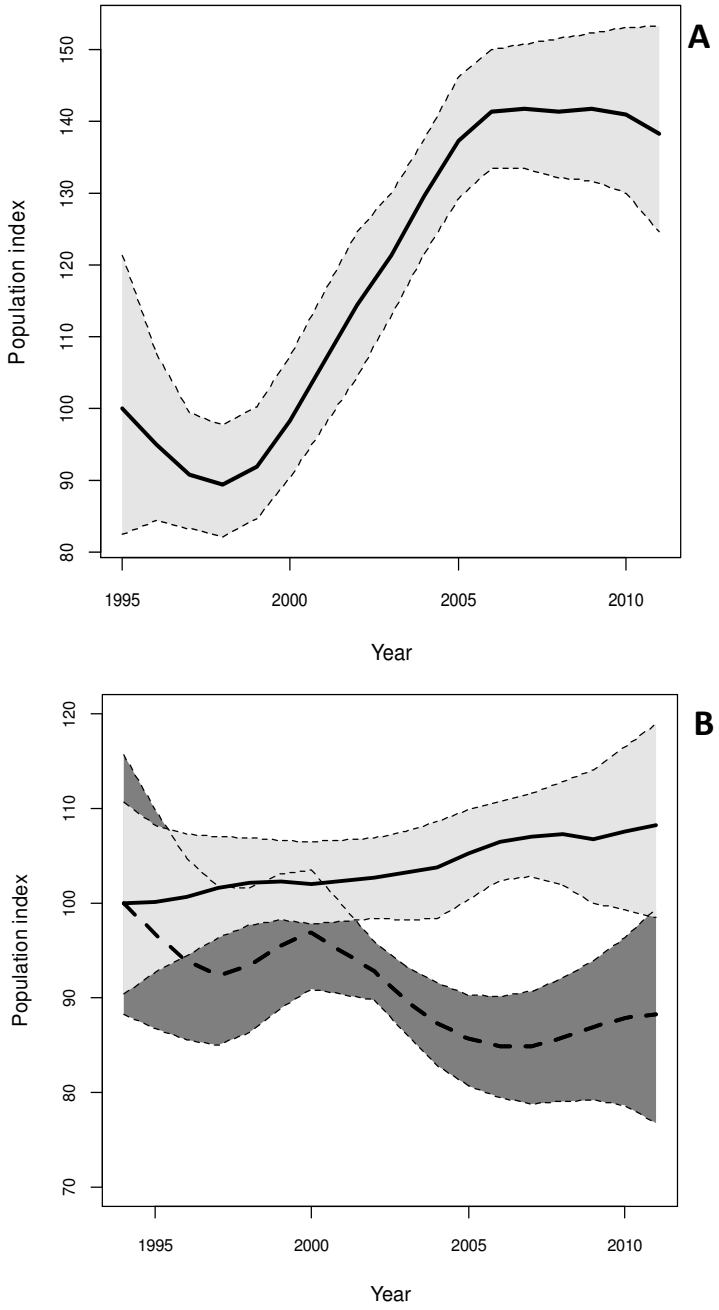


Figure 6-2. Composite population trends of deer and birds. The bold lines show the geometric mean of the individual species population trends. Anything above an index of 100 represents an increase in the index relative to the start year, and *vice versa*. The shaded polygons represent the 90% bootstrap confidence intervals for annual values, from 10,000 bootstrapped replicates (Gregory et al. 2009). (A) Change in the composite population trends for fallow, roe and muntjac deer, in relation to population size in 1995. (B) Changes in the composite population trends of deer-sensitive (*n* = 15) and deer-tolerant (*n* = 16) birds, in relation to population sizes in 1994. The dark grey polygon and the thick dashed line represent deer-sensitive bird species, while the light grey polygon and the solid line represent deer-tolerant species.

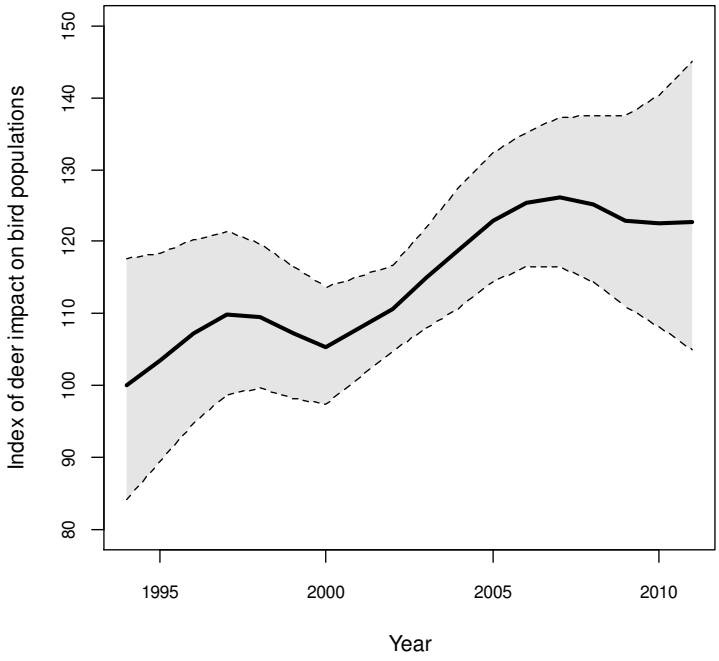


Figure 6-3. The Deer Impact Indicator (solid black line) is the ratio of the composite population index for deer-tolerant birds to that of deer-sensitive birds. The bold lines show the geometric mean of the Deer Impact Indicator. Anything above an index of 100 represents an increase in the index relative to the start year, and vice versa. The shaded polygons represent the 90% bootstrap confidence intervals for annual values, from 10,000 bootstrapped replicates (Gregory et al. 2009).

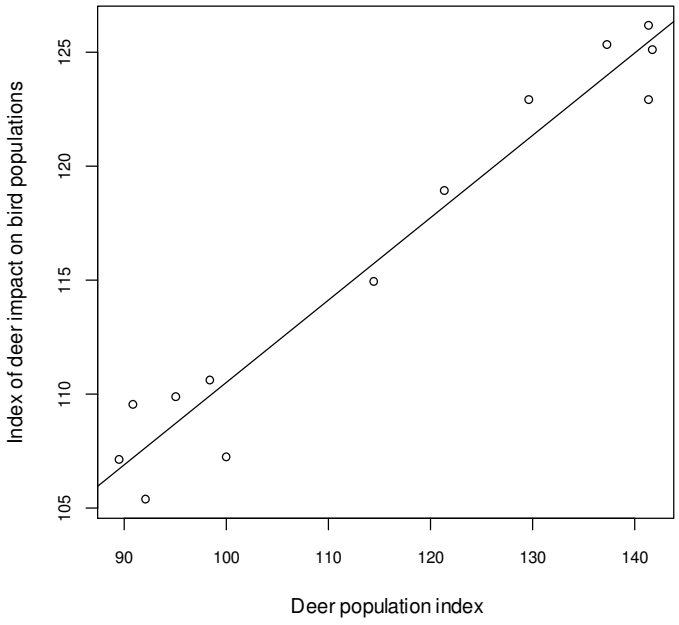


Figure 6-4. Correlation between deer population index and the Deer Impact Indicator.

Table 6-3. Correlations between the Deer Impact Indicator (DII) and climate- and deer trends. Spearman's rank correlations accounting for time lags of between 0 and 3 years were tested. No significant correlations were found between the DII and climate trends (growing degree days above 5°C [GDD5] or mean temperature of the coldest month [MTCO]). Significant correlations were observed between the DII and the deer index. Generalised linear models were also fitted to each set of parameters with the corresponding time lags; the most parsimonious model (with the lowest AIC) for each relationship is highlighted in bold.

Parameters	Lag (years)	Correlation coefficient	*S*	*p*	ΔAIC
DII, Deer	0	0.82	66	<0.01	13.40
	1	0.92	30	<0.01	0.00
	2	0.87	48	<0.01	11.20
	3	0.69	114	0.01	23.40
DII, GDD5	0	0.10	76	0.84	9.20
	1	0.31	58	0.46	9.70
	2	0.31	58	0.46	6.60
	3	0.10	76	0.84	0.00
DII, MTCO	0	0.40	50	0.33	8.80
	1	0.33	56	0.43	7.00
	2	0.57	36	0.15	0.00
	3	0.14	72	0.75	1.70

6.5. Discussion

Recent increases in deer populations across Britain appear to be strongly related to decreases in the abundance of woodland bird populations dependent on understorey vegetation for food and/or nesting opportunities. The DII, which reflects the divergence in composite population indices of birds expected to be impacted by deer and those not expected to be impacted by deer, showed a very strong, significant positive correlation with the composite population trend of deer within the study sites (Figure 6-4, Table 6-3). That finding accords with the expectation that deer have a delayed impact on understorey bird populations (Hewson and Noble 2009), through

indirect impacts on shrub layer vegetation as a result of herbivory (Fuller 2001, Côté et al. 2004, Holt et al. 2011).

Within the deer-sensitive and deer-tolerant bird species groups, individual population trends were not unidirectional (Table 6-2). However, as predicted, populations of deer-sensitive bird species, considered together, declined significantly by 9% between 1995 and 2010, while populations of deer-tolerant bird species increased significantly by 7% over the same time period (Figure 6-2). Deer-sensitive species suffered a decline between 2000 and 2007, and the link with increases in deer abundance since 1998 (Figure 6-2) is a compelling suggestion of causation. Both the DII (Figure 6-3) and the deer population trend (Figure 6-2) increased throughout the early 2000s. However, since 2006 deer abundance in the study sites appears to have stabilised. The one-year time lag between changes in deer population trend and in the DII is illustrated by the stabilisation of the DII since 2007. Whether this close correlation persists over coming years will be a strong test of the indicator.

Observed intra-group differences in individual population trends show that the choice of bird species to include would have a bearing on the DII (Table 6-2). However, four factors provide reassurance that this would not change my conclusions. First, I limited the bird species included in the index only to those independently classified as 'woodland birds' (DEFRA 2011), as I expected deer to have a pronounced effect on woodland species (Newson et al. 2012). Second, I grouped birds into deer-tolerant and deer-sensitive species in line with previous studies (Hewson and Noble 2009, Newson et al. 2012), according to known habitat, feeding and/or nesting preferences. Third, bootstrapped confidence intervals around the DII suggest that the index is robust to variation in the chosen species. Fourth, while there is variation in individual population trends within my two groups of birds, this is both unsurprising and relatively unimportant to my broader conclusions. In particular, it is likely that competition occurs between bird species within each of the two groups, potentially resulting in trends for some species that are counter to expectation. As a result, it is important to focus on the overall fate of each group of species, rather than single species trends.

Although I cannot attribute causality with complete confidence based on these observational data, my focus on the contrasting fates of two sympatric groups of

species controls for many potential confounding processes. Unmeasured factors that have been shown to influence woodland bird populations include changes in the age structure and/or management of woodlands (Hewson and Noble 2009), processes affecting other habitat types (Hewson et al. 2007), such as in agricultural landscapes, or even recent climate changes (Both et al. 2006). However, I found no support for the role of alternative drivers in determining observed bird population changes in the DII. Specifically, I found no evidence for climatic influences on the DII (Table 6-3), and, unfortunately, there is a lack of available data to ascertain whether land-use or land-management changes have affected species abundances. Furthermore, although nearly half of the birds in the deer-sensitive group were migrants (Table 6-1), the composite population trends for migrants and non-migrants in the deer-sensitive group followed the same temporal trend (Figure S 3, page 174). Consequently, the change in the DII cannot be attributed to migratory birds driving down the composite trend of deer-sensitive birds. Producing an index based *a-priori* on species vulnerable and tolerant to deer and then demonstrating consistent divergence in their population trends is a compelling argument for deer being a major contributor to these recent trends.

I have shown that recent changes in the abundance of woodland bird populations vulnerable to the impacts of deer are strongly associated with preceding changes in deer populations. These results provide insight into the rapid, landscape-scale impacts deer can have on avian community structure. In light of widespread, on-going increases in herbivorous ungulates (Rooney and Waller 2003, Ward 2005, Newson et al. 2012, Wäber et al. 2013), significant ecological changes will arise. Land managers must anticipate these changes, either accepting the dynamic nature of systems under their care, or adapting management strategies in light of the likely impacts on species of economic, ecological or cultural importance. However, care must be taken in deciding on management decisions using the DII: management to stabilise or reverse the trend of declining deer-sensitive woodland birds – such as by increasing deer culls or increasing woodland planting – may have the simultaneous, negative effect of reducing abundances of species which rely on open habitats, such as the wood warbler and tree pipit. The DII should therefore be seen as a tool which can, using available

data, rapidly help to identify when further investigation may be required to guide management decisions when deer are suspected of negatively affecting the abundance and composition of woodland bird communities.

Chapter 7 : General discussion

This thesis has covered two main themes: (1) the development of a spatially explicit population model (SEPM) to predict the recent and potential future spread of species across a heterogeneous environment and (2) an investigation into the impacts of keystone herbivores on their environment. Here, I discuss the findings and novelty of this research, including recommendations for future research within these two themes and conclude by setting this research in a broader ecological context.

7.1. Summary of findings

As I stated in Chapter 1, in order to manage populations of deer effectively, it is important to quantify and understand the mechanisms behind changes in their distribution and/or abundances. As such, the aim of the first section of this thesis was to develop models to predict the future distribution of deer, and to identify factors influencing their spread.

7.1.1. Predicting the spread of deer across a heterogeneous environment

Correlative models are the most widely used approach for modelling current and potential future species distributions (Beerling et al. 1995, Araujo and Guisan 2006, Thuiller et al. 2006a). However, such models often violate the assumption that species are at equilibrium with their environment. For example, as deer distributions have expanded in many temperate regions across the globe in recent decades (Côté et al. 2004, Dolman and Waber 2008), it may be erroneous to assume that areas currently unoccupied are environmentally unsuitable for these species. Therefore, in Chapter 2, I developed a novel habitat suitability model for deer, which accounts for dis-equilibrium between species and their environments. For my study species in Britain, I found that there were large expanses of environmentally suitable habitat not currently occupied, which highlights the *potential* for these species to expand their ranges in the future. Such correlative models can be used to identify environmentally suitable areas but cannot predict if, or when, a species may occupy those areas, as they do not take into account range-limiting processes. In Chapters 3 and 4, therefore, I combined the output of static habitat suitability models (Chapter 2) with data on species-specific traits such as fecundity and dispersal distances (Appendix 2) into a SEPM, to predict the spread and future distribution of deer in Britain.

The results presented in Chapter 4 are a first attempt to predict the future rate of spread and pattern of deer distribution in Britain using a SEPM, and highlight the rapid rate of contemporary expansion and potential future expansion of all species. These results will be of interest to a wide variety of stakeholders – from hunters and site managers to conservation organisations. Roe deer were simulated to occupy virtually all of mainland Britain by 2020, and red and muntjac deer were simulated to nearly double their distribution sizes between 2007 and 2040 (Chapter 4). However, the spread of muntjac by 2040 was predicted to be much less extensive than the area of suitable habitat predicted by correlative habitat suitability models (Figure 2-2 compared to Figure 4-1). As muntjac are a non-native British species, focus should be on preventing their spread into areas predicted to be suitable but where from which the species is currently absent – examples include much of eastern Kent, the north of Wales, Northumberland and Cumbria (Figure 4-1). The difficulty of recording muntjac when they occur at low populations densities may make monitoring of spread at the range edges particularly problematic.

The development of the SEPM (Chapter 3) allowed me to identify species traits that have a strong influence on population spread, as well as gaps in current knowledge of demography for species, and where the collection of more detailed data would be beneficial. Results from sensitivity analyses carried out in Chapter 3 indicate that survival, in particular, influences spread of deer: low survival rates reduce the rate of spread (Figure 3-10, Figure 3-11 and Figure 3-12). This finding supports results from studies of other taxa (Wiegand et al. 2004a, Travis et al. 2011). As climate change is predicted to increase the survival and fecundity of deer (Fuller and Gill 2001, Irvine et al. 2007 in Newson et al. 2012, Moyes et al. 2011), deer may spread even faster than suggested by the results of Chapter 4.

While the SEPM made robust predictions of the distribution of deer (Chapter 3), and have been shown also to simulate the spread butterflies across the U.K. (Kerr 2012), modifications to the model would undoubtedly improve performance. Incorporating spatial and temporal variation in species' traits would allow for improved understanding of how species may respond to environmental change (Kearney and

Porter 2009). In Chapter 5, I also discussed the need for a fuller consideration of deer-vehicle collisions in such models.

In Chapter 3 I showed that dynamic distribution models performed poorly in predicting deer distributions in some locations, most likely as a result of under-recording of observed distributions and because of translocations by humans. Additionally, after a review of the literature (Appendix 2), it became clear that species-specific traits which were required as model inputs in the SEPM were either completely lacking, or came from studies with limited sample sizes, and/or geographic and temporal scope. This is not a phenomenon restricted to ungulates: similar findings have been reported in studies of a wide range of taxa, including beetles (Rushton et al. 1996) and foxes (Devenish-Nelson et al. 2013). Despite concerns over their potential impact on native flora and fauna, it is interesting to note that the three species of non-native deer are particularly poorly studied in Britain.

7.1.1.1. Future research

To aid our understanding of the future potential spread of deer, one area of data deficiency and hence high priority is that of obtaining more detailed information on survival, fecundity and dispersal (probability and distances) of deer. Spatial and temporal variation in these parameters would further improve model performance, and, therefore, confidence in predictions of future distributions. One option to fill this information gap might be to make use of the wealth of data that could be obtained from culled deer. Although the National Gamebag Census is established in the U.K. as a "*central repository of… information from shooting and game-keeping activities*" (www.gwct.org.uk/research/long-term-monitoring/national-gamebag-census/; accessed November 2013), the data collected are limited to the number and species of individual animals shot. Extending the scope of this repository to include data such as the species, location, age, sex, body condition and fecundity of shot individuals would be invaluable, and would allow for the quantification of how demographic parameters vary spatially and temporally. Such data are routinely collected for hunted taxa elsewhere in Europe (e.g. Wauters et al. 1995, Mason et al. 2012) and in a limited number of sites in Britain. Indeed, data from Ministry of Defence and Forestry Commission sites have been used to obtain measures such as foetal sex ratios and

neonatal mortality of roe and muntjac deer in sites across Britain (MacDonald and Johnson 2008, Wäber et al. 2013); these estimates were used as parameter estimates in the SEPM (Chapters 3 and 4). However, the deer culled on such sites are a very limited subset of the total number of deer culled per year across Britain, and the records are spatially biased (the majority from the south of England) (MacDonald and Johnson 2008). Thus, a centralised, accessible repository from a large number of sites across the whole of the U.K. would be an invaluable resource. Another option is to collect data such as survival rates, dispersal distances and habitat-use from radio-tracking experiments. These are regularly employed, particularly across European countries; however, there have been very few, if any, in Britain. The drawbacks of these latter approaches are the large amount of man-hours and resource costs associated with their implementation (Davies and Irvine 2011). However, the outputs are clearly very valuable in studies such as this one.

7.1.2. The impacts of keystone herbivores on their environment

In the absence of management, the continued spread of deer into areas where they are currently absent, or increase in density in places where they are currently found, may have important implications for community composition. As such, there is a growing need to identify and quantify the impacts of deer on their environments, especially given that they often act as keystone herbivores in the ecosystems they occupy (Cumming et al. 1997, Rooney and Waller 2003, Côté et al. 2004). In order to investigate these impacts, I carried out fieldwork to quantify the impact of roe deer on woodland vegetation (Chapter 5).

Although variation between field sites was high, significant negative relationships between roe deer density and both shrub layer diversity and cover were observed (Chapter 5). These results are similar to those reported by other authors (Putman et al. 1989, Fuller 2001, Gill and Beardall 2001, Joys et al. 2004, Sage et al. 2004, Gill and Fuller 2007, Gill and Morgan 2010). However, as I carried out fieldwork in sites containing only roe deer, I have been able to demonstrate, for the first time, the likely impact of this species on vegetation structure and composition in British woodland, based on data from multiple sites and across a range of natural deer densities.

In Chapter 6, I investigated the cascading impacts of herbivores on bird communities at a national scale by investigating the temporal trends of birds and deer. I found a striking relationship between the temporal population trend of deer with that of the divergence in trends of deer-tolerant and deer-sensitive birds, highlighting the rapid knock-on effects deer may have on bird species that rely on understorey vegetation. Other authors have reported reductions in the abundance of bird species dependent on understorey vegetation in response to increased deer browsing (Degraaf et al. 1991, deCalesta 1994, McShea and Rappole 2000, Perrins and Overall 2001, Allombert et al. 2005a), but these previous studies have tended to be limited in temporal or spatial scope, focussing on a small number species and/or locations. One North American study reported that the population trends of breeding birds dependent on shrub and/or ground layer vegetation declined over time (Baiser et al. 2008); while these authors postulated that overabundant white-tailed deer were driving the reduction in abundance of these shrub-layer-dependent birds, they did not take the next step and relate temporal trends of birds to those of deer. If deer populations continue to expand as predicted in Chapter 4, it is expected that impacts on biodiversity will also increase. It will be interesting to see if this occurs in future, and the indicator developed in Chapter 6 provides an easily-interpretable approach to visualise temporal changes in environmental drivers and the components of biodiversity they (are expected to) influence.

It is important to note that factors other than increasing deer populations will have impacts on components of biodiversity such as birds. Additive factors such as a reduction in woodland management and processes affecting other habitat types have also been shown to influence woodland vegetation and, consequently, understorey bird populations (Fuller et al. 2005). However, the lack of quantitative data on how factors such as woodland management have varied across the spatial and temporal resolution of my study precluded their inclusion in the analyses of Chapters 5 and 6. Despite these limitations, other studies have corroborated my findings, demonstrating the influence of increasing deer density on populations of individual woodland bird species, across large spatial scales (Newson et al. 2012). Furthermore, in Chapter 5 I showed that as deer density increases, shrub layer diversity and abundance decreased.

This lends more support to the finding that the populations of deer-sensitive birds reliant on the shrub layer vegetation decline as deer density increases.

7.1.2.1. Future research

I was unable to explicitly investigate the relationships between deer density, impacts on vegetation, and knock-on impacts on other components of biodiversity within the same field sites. This would require data to be collected at numerous sites – more than the 35 field sites used in the analyses of Chapter 5. An exciting and simple solution to this problem would be to incorporate the collection of simple vegetation metrics into Breeding Bird Surveys (BBS) – as a minimum, BBS volunteers would need to report estimates of the percentage cover of shrub layer vegetation, alongside the bird and mammal count data already collected.

The scope of the analyses presented in Chapter 6 could be extended by investigating the influence of different woodland- and deer management strategies on the DII. For example, once such data are available, one could split sites up into those under different ownership and therefore with different deer management strategies (Austin et al. 2010). One might expect that in sites where deer are managed at stable levels across time, impacts on temporal trends of understorey birds, and therefore the DII, would also be stable, and *vice versa*.

It would be interesting to investigate whether the same relationships between roe deer density and shrub layer diversity and abundance (observed in Chapter 5) are also observed if focussed on sites with only muntjac deer – which are similar to roe deer in body size and feeding ecology. As discussed in Chapter 5, roe deer have the potential to change successional trajectories of woodlands, by changing shrub-layer vegetation dynamics. This may have implications across ecosystems in the longer-term, which could be investigated with long-term follow-up experiments in the field sites where data were originally collected. Such long-term experiments are rarely carried out, but those that have (e.g. Nuttle et al. 2014) have reported significant negative effects of high deer density on vegetation cover over multiple decades.

7.2. Implications of my findings for deer management

While it is important to note that not all impacts of deer are negative, it is also the case that populations of deer in temperate regions across the globe are reaching levels unprecedented in recent times. As such, there will undoubtedly be increased focus on the negative impacts of these species when they occur at high densities. Therefore, a focus of deer management should be to monitor and control the spread of deer into areas where there may be conflict between deer and sensitive species or habitats. Accordingly, one aim of this research was to identify locations where British deer may colonise in the future (section 7.1.1), and therefore where (increased) management may be required to control cascading negative impacts, but also to maintain healthy deer populations. While I have described previously the locations where species-specific deer management may be required in Britain (section 7.1.1), the spread of deer is not a phenomenon restricted to Britain. Accordingly, SEPMs such as the one developed here, could be adapted for other species and locations in order to aid species' management in the future.

Managers should also be aware of the potential for deer to spread even further than predicted (by models such as the one developed here), as a result of factors such as changing environmental suitability and the release or escape of deer from collections. Certainly, deer held within collections should be regularly monitored and highly controlled to prevent their escape or release – registration of collections has previously been suggested (Ward and Lees 2011) to address this issue. Deer management will need to take a landscape-scale approach (Putman et al. 2011b), with a rapid response to changes in population density and spread into new areas so that negative impacts are controlled and/or prevented. Such a response will rely on regular and thorough monitoring of deer, as well as reliable predictions of the rate and patterns of spread. Deer distribution and abundance surveys are an invaluable source of data in this regard, and should be continued.

Although it is likely that some species will benefit from the predicted increase in the range and abundance of deer, I have provided evidence in Chapters 5 and 6 that the impact deer are having on their environment is now at damaging levels, influencing many species across a range of trophic levels. I found no evidence for a threshold deer

density above which impacts were especially damaging. Therefore, instead of management focussed at controlling deer population densities at a pre-prescribed level, management should take a combined approach of monitoring impacts as well as deer density (Putman et al. 2011a).

7.3. General conclusions

Species across the world have been shown to be shifting in response to environmental drivers such as land use change, or climate change (Root et al. 2003, Parmesan 2006). It is important to obtain predictions of these changing distributions so that conservation measures such as management of invasive species, or translocation of threatened species, can be put in place in the most appropriate locations. In Chapters 2 to 4, I demonstrated the strengths and limitations of using correlative and mechanistic distribution models to predict species distributions, and corroborated the findings of other authors (e.g. Huntley et al. 2010): where data allows, mechanistic models should preferentially be used to predict future distributions and therefore to identify areas to target species' management. However, in situations where data limitations prevent the use of mechanistic models, dis-equilibrium between species and their environment should be taken into account within 'traditional' correlative approaches, so that more robust predictions of potential range changes can be made.

Inevitably, as species distributions and abundances change, impacts on their environments will also change. The methodology used in Chapter 6 has been used previously to demonstrate the impact of climate change on European bird populations (Gregory et al. 2009). Here, I have shown that this methodology can easily be adapted to investigate other environmental drivers of population change including the cascading influence of herbivores on biodiversity. As communities alter as a result of changes in species distribution and abundances, the methodology described in Chapter 6 could become a useful tool in determining the cascading influence of herbivores in other environments. For example, it could be used to investigate the potential role of kangaroo *Macropus giganteus* on bird communities in Australia, given the observed impact of this species on understorey-dependent birds (Australian Capital Territory 2010). Similarly, it could be applied to other deer species in temperature regions across the globe, such as white-tailed deer in America and the red and roe deer in

other European counties. Moreover, the use of this methodology could be extended to investigate scenarios such as the influence of the reintroduction of predators on species within their new environments.

Although predictive browse models have been created (e.g. Weisberg et al. 2002, Holland et al. 2013, Tanentzap et al. 2013), such models generally cover local or regional scales given the difficulties in parameterising such a model at a large geographic scale. Similarly, empirical studies of impact have generally been limited in temporal or spatial scope. In Chapters 5 and 6, I demonstrated the cascading impacts of deer on vegetation and on bird communities across large temporal and spatial scales. While predicting future impacts was beyond the scope of this work, predictive models to investigate species' impacts could potentially be incorporated into spatially-explicit mechanistic models of spread to investigate and predict the influence of species' distribution and abundance changes on other components of environment.

References

Abernathy, K. 1994. The establishment of a hybrid zone between red and sika deer (genus *Cervus*). Molecular Ecology **3**:551-562.

Acevedo, P., M. Angel Farfan, A. Luz Marquez, M. Delibes-Mateos, R. Real, and J. Mario Vargas. 2011. Past, present and future of wild ungulates in relation to changes in land use. Landscape Ecology **26**:19-31.

Acevedo, P., A. I. Ward, R. Real, and G. C. Smith. 2010. Assessing biogeographical relationships of ecologically related species using favourability functions: a case study on British deer. Diversity and Distributions **16**:515-528.

Aebischer, N. J., P. D. Davey, and N. G. Kingdon. 2011. National Gamebag Census: Mammal Trends to 2009. Game & Wildlife Conservation Trust, Fordingbridge (www.gwct.org.uk/ngcmammals).

Akashi, N., A. Unno, and K. Terazawa. 2011. Effects of deer abundance on broad-leaf tree seedling establishment in the understory of Abies sachalinensis plantations. Journal of Forest Research **16**:500-508.

Albon, S. D., T. H. Cluttonbrock, and F. E. Guinness. 1987. Early development and population dynamics in red deer. 2. Density-independent effects and cohort variation. Journal of Animal Ecology **56**:69-81.

Albon, S. D., F. E. Guinness, and T. H. Cluttonbrock. 1983. The influence of climatic variation on the birth weights of red deer (*Cervus elaphus*). Journal of Zoology **200**:295-298.

Allombert, S., A. J. Gaston, and J. L. Martin. 2005a. A natural experiment on the impact of overabundant deer on songbird populations. Biological Conservation **126**:1-13.

Allombert, S., S. Stockton, and J. L. Martin. 2005b. A natural experiment on the impact of overabundant deer on forest invertebrates. Conservation Biology **19**:1917-1929.

Allouche, O., A. Tsoar, and R. Kadmon. 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). Journal of Applied Ecology **43**:1223-1232.

Anderson, B. J., H. R. Akcakaya, M. B. Araujo, D. A. Fordham, E. Martinez-Meyer, W. Thuiller, and B. W. Brook. 2009. Dynamics of range margins for metapopulations under climate change. Proceedings of the Royal Society B-Biological Sciences **276**:1415-1420.

Anderson, R. P., A. T. Peterson, and M. Gomez-Laverde. 2002. Using niche-based GIS modeling to test geographic predictions of competitive exclusion and competitive release in South American pocket mice. Oikos **98**:3-16.

Angold, P. G., J. P. Sadler, M. O. Hill, A. Pullin, S. Rushton, K. Austin, E. Small, B. Wood, R. Wadsworth, R. Sanderson, and K. Thompson. 2006. Biodiversity in urban habitat patches. Science of the Total Environment **360**:196-204.

Apollonio, M., R. Andersen, and R. Putman. 2008. European ungulates and their management in the 21st Century. Cambridge University Press, Cambridge.

Araujo, M. B. and A. Guisan. 2006. Five (or so) challenges for species distribution modelling. Journal of Biogeography **33**:1677-1688.

Araujo, M. B., W. Thuiller, and R. G. Pearson. 2006. Climate warming and the decline of amphibians and reptiles in Europe. Journal of Biogeography **33**:1712-1728.

Arnold, H. R. 1984. Distribution maps of the mammals of the British Isles. Biological Records Centre.

Arnold, H. R. 1992. Atlas of mammals in Britain. HMSO, London.

Atkinson, M. D. and E. Atkinson. 2002. Sambucus nigra L. Journal of Ecology **90**:895-923.

Austin, Z., J. C. R. Smart, S. Yearley, R. J. Irvine, and P. C. L. White. 2010. Identifying conflicts and opportunities for collaboration in the management of a wildlife resource: a mixed-methods approach. Wildlife Research **37**:647-657.

Australian Capital Territory. 2010. ACT Kangeroo Management Plan. ACT, Canberra.

Baines, D., R. B. Sage, and M. M. Baines. 1994. The implications of red deer grazing to ground vegetation and invertebrate communities of Scottish native pinewoods. Journal of Applied Ecology **31**:776-783.

Baiser, B., J. L. Lockwood, D. La Puma, and M. F. J. Aronson. 2008. A perfect storm: two ecosystem engineers interact to degrade deciduous forests of New Jersey. Biological Invasions **10**:785-795.

Baker, K. H. 2011. Population genetic history of the British roe deer (*Capreolus capreolus*) and its implications for diversity and fitness. Ph.D. Durham University.

Ballon, P., B. Guibert, J. P. Hamard, and Y. Boscardin. 1992. Evolution of roe deer browsing pressure in the forest of Dourdan. Ongules / Ungulates **91**:513-518.

Bar-David, S., D. Saltz, and T. Dayan. 2005. Predicting the spatial dynamics of a reintroduced population: The Persian fallow deer. Ecological Applications **15**:1833-1846.

Bartos, L., D. Vankova, K. V. Miller, and J. Siler. 2002. Interspecific competition between white-tailed, fallow, red, and roe deer. Journal of Wildlife Management **66**:522-527.

Beerling, D. J., B. Huntley, and J. P. Bailey. 1995. Climate and the distribution of *Fallopica japonica* - use of an introduced species to test the predictive capacity of response surfaces. Journal of Vegetation Science **6**:269-282.

Benes, J., O. Cizek, J. Dovala, and M. Konvicka. 2006. Intensive game keeping, coppicing and butterflies: The story of Milovicky Wood, Czech Republic. Forest Ecology and Management **237**:353-365.

Bobek, B., K. Perzanowski, J. Siwanowicz, and J. Zielinski. 1979. Deer pressure on forage in a deciduous forest. Oikos **32**:373-380.

Bonenfant, C., J. M. Gaillard, F. Klein, and A. Loison. 2002. Sex- and age-dependent effects of population density on life history traits of red deer *Cervus elaphus* in a temperate forest. Ecography **25**:446-458.

Bonte, D., H. Van Dyck, J. M. Bullock, A. Coulon, M. Delgado, M. Gibbs, V. Lehouck, E. Matthysen, K. Mustin, M. Saastamoinen, N. Schtickzelle, V. M. Stevens, S. Vandewoestijne, M. Baguette, K. Barton, T. G. Benton, A. Chaput-Bardy, J. Clobert, C. Dytham, T. Hovestadt, C. M. Meier, S. C. F. Palmer, C. Turlure, and J. M. J. Travis. 2012. Costs of dispersal. Biological Reviews **87**:290-312.

Both, C., S. Bouwhuis, C. M. Lessells, and M. E. Visser. 2006. Climate change and population declines in a long-distance migratory bird. Nature **441**:81-83.

Bressette, J. W., H. Beck, and V. B. Beauchamp. 2012. Beyond the browse line: complex cascade effects mediated by white-tailed deer. Oikos **121**:1 - 12.

British Deer Society. 2010a. Chinese Water Deer: http://www.bds.org.uk/chinese_water_deer.html. British Deer Society.

British Deer Society. 2010b. Fallow Deer: http://www.bds.org.uk/fallow.html. British Deer Society.

British Deer Society. 2010c. Muntjac Deer: http://www.bds.org.uk/muntjac.html. British Deer Society.

British Deer Society. 2010d. Red Deer: http://www.bds.org.uk/red_deer.html. British Deer Society.

British Deer Society. 2010e. Roe Deer: http://www.bds.org.uk/roe.html.

British Deer Society. 2010f. Sika Deer: http://www.bds.org.uk/sika.html. British Deer Society.

Broennimann, O., U. A. Treier, H. Muller-Scharer, W. Thuiller, A. T. Peterson, and A. Guisan. 2007. Evidence of climatic niche shift during biological invasion. Ecology Letters **10**:701-709.

Brotons, L., W. Thuiller, M. B. Araujo, and A. H. Hirzel. 2004. Presence-absence versus presence-only modelling methods for predicting bird habitat suitability. Ecography **27**:437-448.

Bruinderink, G. and E. Hazebroek. 1996. Ungulate traffic collisions in Europe. Conservation Biology **10**:1059-1067.

Brunet, J., U. FalkengrenGrerup, and G. Tyler. 1996. Herb layer vegetation of south Swedish beech and oak forests - Effects of management and soil acidity during one decade. Forest Ecology and Management **88**:259-272.

Bullock, D. J. 2009. What larger mammals did Britain have and what did they do? British Wildlife **20**:16-20.

Cardinal, E., J.-L. Martin, J.-P. Tremblay, and S. D. Cote. 2012. An experimental study of how variation in deer density affects vegetation and songbird assemblages of recently harvested boreal forests. Canadian Journal of Zoology-Revue Canadienne De Zoologie **90**:704-713.

Carne, P. 2000. Deer of Britain and Ireland: their origins and distribution. 1 edition. Swan Hill Press.

Casey, D. and D. Hein. 1983. Effects of heavy browsing on a bird community in deciduous forest. Journal of Wildlife Management **47**:829-836.

Chaplin, R. E. 1977. Deer. Blandford Press, Poole.

Chapman, N., S. Harris, and A. Stanford. 1994. Reeves muntjac *Muntiacus reevesi* in Britain - their history, spread, habitat selection, and the role of human intervention in accelerating their dispersal. Mammal Review **24**:113-160.

Chapman, N. G. and D. I. Chapman. 1980. The distribution of fallow deer - a worldwide review. Mammal Review **10**:61-138.

Chapman, N. G., M. Furlong, and S. Harris. 1997. Reproductive strategies and the influence of date of birth on growth and sexual development of an aseasonally-breeding ungulate: Reeves' muntjac (Muntiacus reevesi). Journal of Zoology **241**:551-570.

Chollet, S. and J. L. Martin. 2013. Declining woodland birds in North America: should we blame Bambi? Diversity and Distributions **19**:481 - 483.

Chu, C., N. E. Mandrak, and C. K. Minns. 2005. Potential impacts of climate change on the distributions of several common and rare freshwater fishes in Canada. Diversity and Distributions **11**:299-310.

Citta, J. J. and L. S. Mills. 1999. What do demographic sensitivity analyses tell us about controlling brown-headed cowbirds? Studies in Avian Biology **18**:121-134.

Clutton-Brock, T. H. and T. Coulson. 2002. Comparative ungulate dynamics: the devil is in the detail. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences **357**:1285-1298.

Clutton-Brock, T. H., T. N. Coulson, E. J. Milner-Gulland, D. Thomson, and H. M. Armstrong. 2002. Sex differences in emigration and mortality affect optimal management of deer populations. Nature **415**:633-637.

Clutton-Brock, T. H. and M. E. Lonergan. 1994. Culling regimes and sex-ratio biases in highland red deer. Journal of Applied Ecology **31**:521-527.

Clutton-Brock, T. H., K. E. Rose, and F. E. Guinness. 1997. Density-related changes in sexual selection in red deer. Proceedings: Biological Sciences **264**:1509-1516.

Cobben, M. M. P., J. D. C. Linnell, E. J. Solberg, and R. Andersen. 2009. Who wants to live forever? Roe deer survival in a favourable environment. Ecological Research **24**:1197-1205.

Collingham, Y. C., M. O. Hill, and B. Huntley. 1996. The migration of sessile organisms: A simulation model with measurable parameters. Journal of Vegetation Science **7**:831-846.

Conroy, M. J., Y. Cohen, F. C. James, Y. G. Matsinos, and B. A. Maurer. 1995. Parameter-estimation, reliability, and model improvement for spatially explicit models of animal populations. Ecological Applications **5**:17-19.

Cooke, A., C. Quine, R. Shore, and R. Trout. 2004. Muntjac and conservation woodlands. Managing woodlands and their mammals: proceedings of a a symposium organised jointly by the Mammal Society and the Forestry Commission:65-69.

Cooke, A. S. 1997. Effects of grazing by muntjac (*Muntiacus reevesi*) on bluebells (*Hyacinthoides non-scripta*) and a field technique for assessing feeding activity. Journal of Zoology **242**:365-369.

Cooke, A. S. and L. Farrell. 2001. Impact of muntjac deer (*Muntiacus reevesi*) at Monks Wood National Nature Reserve, Cambridgeshire, eastern England. Forestry **74**:241-250.

Cooke, A. S., L. Farrell, K. J. Kirby, and R. C. Thomas. 1995. Changes in abundance and size of dog's mercury apparently associated with grazing by muntjac. Deer **9**:429-433.

Cooke, A. S., P. Green, and N. G. Chapman. 1996. Mortality in a feral population of muntjac Muntiacus reevesi in England. Acta Theriologica **41**:277-286.

Cooke, A. S. and K. H. Lakhani. 1996. Damage to coppice regrowth by muntjac deer Muntiacus reevesi and protection with electric fencing. Biological Conservation **75**:231-238.

Corbet, G. B. and S. Harris. 1991. The handbook of British mammals. Blackwell Scientific Publications, Oxford.

Corney, P. M., K. J. Kirby, D. M. G. Le, S. M. Smart, H. A. McAllister, and R. H. Marrs. 2008. Changes in the field-layer of Wytham Woods - assessment of the impacts of a range of environmental factors controlling change. Journal of Vegetation Science **19**:287-U215.

Côté, S. D., T. P. Rooney, J. P. Tremblay, C. Dussault, and D. M. Waller. 2004. Ecological impacts of deer overabundance. Annual Review of Ecology Evolution and Systematics **35**:113-147.

Cottam, G., J. T. Curtis, and B. W. Hale. 1953. Some sampling characteristics of a population of randomly dispersed individuals. Ecology **34**:741-757.

Coulson, T., S. Albon, F. Guinness, J. Pemberton, and T. CluttonBrock. 1997. Population substructure, local density, and calf winter survival in red deer (*Cervus elaphus*). Ecology **78**:852-863.

Cribari-Neto, F. and A. Zeileis. 2010. Beta regression in R. Journal of Statistical Software **34**:1 - 24.

Crick, H. Q. P., C. Dudley, D. E. Glue, and D. L. Thomson. 1997. UK birds are laying eggs earlier. Nature **388**:526-526.

Cumming, D. H. M., M. B. Fenton, I. L. Rautenbach, R. D. Taylor, G. S. Cumming, M. S. Cumming, J. M. Dunlop, A. G. Ford, M. D. Hovorka, D. S. Johnston, M. Kalcounis, Z. Mahlangu, and C. V. R. Portfors. 1997. Elephants, woodlands and biodiversity in southern Africa. South African Journal of Science **93**:231-236.

Daniels, M. and C. McClean. 2003. Red deer calf tagging programmes in Scotland - an analysis. Deer **12**:420-423.

Danilkin, A. and A. J. M. Hewison. 1996. Behavioural ecology of Siberian and European roe deer. Chapman and Hall.

Davies, A. and R. J. Irvine. 2011. Cumbria report - an integrated approach to deer management. Report to Deer Initiative.

De Marco, P., J. A. F. Diniz, and L. M. Bini. 2008. Spatial analysis improves species distribution modelling during range expansion. Biology Letters **4**:577-580.

Debeffe, L., N. Morellet, B. Cargnelutti, B. Lourtet, R. Bon, J.-M. Gaillard, A. J. Mark Hewison, and J. Fryxell. 2012. Condition-dependent natal dispersal in a large herbivore: heavier animals show a greater propensity to disperse and travel further. Journal of Animal Ecology **81**:1327-1327.

deCalesta, D. S. 1994. Effect of white-tailed deer on songbirds within managed forests in Pennsylvania. Journal of Wildlife Management **58**:711-718.

DEFRA. 2011. Wild bird populations in England, 1970 - 2011. Department for Environment, Food and Rural Affairs.

DeGabriel, J. L., S. D. Albon, D. A. Fielding, D. J. Riach, S. Westaway, and R. J. Irvine. 2011. The presence of sheep leads to increases in plant diversity and reductions in the impact of deer on heather. Journal of Applied Ecology **48**:1269-1277.

Degraaf, R. M., W. M. Healy, and R. T. Brooks. 1991. Effects of thinning and deer browsing on breeding birds in New-England oak woodlands. Forest Ecology and Management **41**:179-191.

Devenish-Nelson, E. S., S. Harris, C. D. Soulsbury, S. A. Richards, and P. A. Stephens. 2013. Demography of a carnivore, the red fox, *Vulpes vulpes*: what have we learnt from 70 years of published studies? Oikos **122**:705-716.

Diaz, A., E. Pinn, J. Hannaford, J. Humphreys, and V. May. 2005. Ecological impacts of sika deer on Poole Harbour saltmarshes. Proceedings in Marine Science **7**:175-188.

Dolman, P., R. Fuller, R. Gill, D. Hooton, and R. Tabor. 2010. Escalating ecological impacts of deer in lowland woodland. British Wildlife **21**:242-254.

Dolman, P. M. and K. Waber. 2008. Ecosystem and competition impacts of introduced deer. Wildlife Research **35**:202-214.

Dunning, J. B., D. J. Stewart, B. J. Danielson, B. R. Noon, T. L. Root, R. H. Lamberson, and E. E. Stevens. 1995. Spatially explicit population models: current forms and future uses. Ecological Applications **5**:3-11.

Elith, J., C. H. Graham, R. P. Anderson, M. Dudik, S. Ferrier, A. Guisan, R. J. Hijmans, F. Huettmann, J. R. Leathwick, A. Lehmann, J. Li, L. G. Lohmann, B. A. Loiselle, G. Manion, C. Moritz, M. Nakamura, Y. Nakazawa, J. M. Overton, A. T. Peterson, S. J. Phillips, K. Richardson, R. Scachetti-Pereira, R. E. Schapire, J. Soberon, S. Williams, M. S. Wisz, and N. E. Zimmermann. 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography **29**:129-151.

Elith, J., M. Kearney, and S. Phillips. 2010. The art of modelling range-shifting species. Methods in Ecology and Evolution **1**:330-342.

Elith, J. and J. R. Leathwick. 2009. Species distribution models: Ecological explanation and prediction across space and time. Annual Review of Ecology Evolution and Systematics **40**:677-697.

Eycott, A. E., A. R. Watkinson, M. R. Hemami, and P. M. Dolman. 2007. The dispersal of vascular plants in a forest mosaic by a guild of mammalian herbivores. Oecologia **154**:107-118.

Feber, R. E., T. M. Brereton, M. S. Warren, and M. Oates. 2001. The impacts of deer on woodland butterflies: the good, the bad and the complex. Forestry **74**:271-276.

Fennell, M., J. E. Murphy, T. Gallagher, and B. Osborne. 2013. Simulating the effects of climate change on the distribution of an invasive plant, using a high resolution, local scale, mechanistic approach: challenges and insights. Global Change Biology **19**:1262-1274.

Fewster, R. M., S. T. Buckland, G. M. Siriwardena, S. R. Baillie, and J. D. Wilson. 2000. Analysis of population trends for farmland birds using generalized additive models. Ecology **81**:1970-1984.

Ficetola, G. F., L. Maiorano, A. Falcucci, N. Dendoncker, L. Boitani, E. Padoa-Schioppa, C. Miaud, and W. Thuiller. 2010. Knowing the past to predict the future: land-use change and the distribution of invasive bullfrogs. Global Change Biology **16**:528-537.

Fielding, A. H. and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation **24**:38-49.

Fitzpatrick, M. C., J. F. Weltzin, N. J. Sanders, and R. R. Dunn. 2007. The biogeography of prediction error: why does the introduced range of the fire ant over-predict its native range? Global Ecology and Biogeography **16**:24-33.

Flowerdew, J. R. and S. A. Ellwood. 2001. Impacts of woodland deer on small mammal ecology. Forestry **74**:277-287.

Focardi, S., P. Aragno, P. Montanaro, and F. Riga. 2006. Inter-specific competition from fallow deer *Dama dama* reduces habitat quality for the Italian roe deer *Capreolus capreolus italicus*. Ecography **29**:407-417.

Forde, P. 1989. Comparative ecology of muntjac (*Muntiacus reevesi*) and roe deer (*Capreolus capreolus*) in a commercial coniferous forest. Ph.D. . University of Bristol.

Fordham, D. A., H. R. Akcakaya, M. B. Araujo, J. Elith, D. A. Keith, R. Pearson, T. D. Auld, C. Mellin, J. W. Morgan, T. J. Regan, M. Tozer, M. J. Watts, M. White, B. A. Wintle, C. Yates, and B. W. Brook. 2012. Plant extinction risk under climate change: are forecast range shifts alone a good indicator of species vulnerability to global warming? Global Change Biology **18**:1357-1371.

Franklin, J. 2010. Moving beyond static species distribution models in support of conservation biogeography. Diversity and Distributions **16**:321-330.

Franklin, J., F. W. Davis, M. Ikegami, A. D. Syphard, L. E. Flint, A. L. Flint, and L. Hannah. 2013. Modeling plant species distributions under future climates: how fine scale do climate projections need to be? Global Change Biology **19**:473-483.

Freeman, E. A. and G. G. Moisen. 2008. A comparison of the performance of threshold criteria for binary classification in terms of predicted prevalence and kappa. Ecological Modelling **217**:48-58.

Freeman, S. N., D. G. Noble, S. E. Newson, and S. R. Baillie. 2007. Modelling population changes using data from different surveys: the common birds census and the breeding bird survey. Bird Study **54**:61-72.

Fuller, R. J. 2001. Responses of woodland birds to increasing numbers of deer: a review of evidence and mechanisms. Forestry **74**:289-298.

Fuller, R. J. and R. M. A. Gill. 2001. Ecological impacts of increasing numbers of deer in British woodland. Forestry **74**:193-199.

Fuller, R. J. and A. C. B. Henderson. 1992. Distribution of breeding songbirds in Bradfield Woods, Suffolk, in relation to vegetation and coppice management. Bird Study **39**:73-88.

Fuller, R. J., D. G. Noble, K. W. Smith, and D. Vanhinsbergh. 2005. Recent declines in populations of woodland birds in Britain: a review of possible causes. British Birds **98**:116-143.

Fuller, R. J., K. W. Smith, P. V. Grice, F. A. Currie, and C. P. Quine. 2007. Habitat change and woodland birds in Britain: implications for management and future research. Ibis **149**:261-268.

Gaillard, J. M., J. M. Boutin, D. Delorme, G. VanLaere, P. Duncan, and J. D. Lebreton. 1997. Early survival in roe deer: causes and consequences of cohort variation in two contrasted populations. Oecologia **112**:502-513.

Gaillard, J. M., D. Delorme, J. M. Boutin, G. Vanlaere, B. Boisaubert, and R. Pradel. 1993. Roe deer survival patterns: a comparative analysis of contrasting populations. Journal of Animal Ecology **62**:778-791.

Gaillard, J. M., A. J. M. Hewison, P. Kjellander, N. Pettorelli, C. Bonenfant, B. Van Moorter, O. Liberg, H. Andren, G. Van Laere, F. Klein, J. M. Angibault, A. Coulon, and C. Vanpe. 2008. Population density and sex do not influence fine-scale natal dispersal in roe deer. Proceedings of the Royal Society B-Biological Sciences **275**:2025-2030.

Gallien, L., R. Douzet, S. Pratte, N. E. Zimmermann, and W. Thuiller. 2012. Invasive species distribution models – how violating the equilibrium assumption can create new insights. Global Ecology and Biogeography **21**:1126 - 1136.

Gasso, N., W. Thuiller, J. Pino, and M. Vila 2012. Potential distribution range of invasive plant species in Spain. NeoBiota **12**:25-40.

Gibbs, E. P. J., K. A. J. Herniman, M. J. P. Lawman, and R. F. Sellers. 1975. Foot-and-mouth disease in British deer: Transmission of virus to cattle, sheep and deer. Veterinary Record **96**:558-563.

Giljohann, K. M., C. E. Hauser, N. S. G. Williams, and J. L. Moore. 2011. Optimizing invasive species control across space: willow invasion management in the Australian Alps. Journal of Applied Ecology **48**:1286 - 1294.

Gill, R. M. A. 1992a. A review of damage by mammals in north temperate forests. 1. Deer. Forestry **65**:145-169.

Gill, R. M. A. 1992b. A review of damage by mammals in north temperate forests. 3. Impact on trees and forests. Forestry **65**:363-388.

Gill, R. M. A. 1994. The population dynamics of roe deer (*Capreolus capreolus* L.) in relation to habitat succession. Ph.D. Open University, U.K.

Gill, R. M. A. 2000. The impact of deer on woodland biodiversity. FCIN36, Forestry Commission.

Gill, R. M. A. and V. Beardall. 2001. The impact of deer on woodlands: the effects of browsing and seed dispersal on vegetation structure and composition. Forestry **74**:209-218.

Gill, R. M. A. and R. J. Fuller. 2007. The effects of deer browsing on woodland structure and songbirds in lowland Britain. Ibis **149**:119-127.

Gill, R. M. A. and G. Morgan. 2010. The effects of varying deer density on natural regeneration in woodlands in lowlands Britain. Forestry **83**:53 - 63.

Gill, R. M. A., M. L. Thomas, and D. Stocker. 1997. The use of portable thermal imaging for estimating deer population density in forest habitats. Journal of Applied Ecology **34**:1273-1286.

Goodman, S. J., N. H. Barton, G. Swanson, K. Abernethy, and J. M. Pemberton. 1999. Introgression through rare hybridization: A genetic study of a hybrid zone between red and sika deer (genus Cervus) in Argyll, Scotland. Genetics **152**:355-371.

Gormley, A. M., D. M. Forsyth, P. Griffioen, M. Lindeman, D. S. L. Ramsey, M. P. Scroggie, and L. Woodford. 2011. Using presence-only and presence-absence data to estimate the current and potential distributions of established invasive species. Journal of Applied Ecology **48**:25-34.

Gormley, A. M., E. Penelope Holland, R. P. Pech, C. Thomson, and B. Reddiex. 2012. Impacts of an invasive herbivore on indigenous forests. Journal of Applied Ecology **49**:1296-1305.

Greenwald, K. R., L. J. Petit, and T. A. Waite. 2008. Indirect effects of a keystone herbivore elevate local animal diversity. Journal of Wildlife Management **72**:1318-1321.

Gregory, R. D. and A. van Strien. 2010. Wild bird indicators: using composite population trends of birds as measures of environmental health. Ornithological Science **9**:3-22.

Gregory, R. D., P. Vorisek, A. Van Strien, A. W. G. Meyling, F. Jiguet, L. Fornasari, J. Reif, P. Chylarecki, and I. J. Burfield. 2007. Population trends of widespread woodland birds in Europe. Ibis **149**:78-97.

Gregory, R. D., S. G. Willis, F. Jiguet, P. Vorisek, A. Klvanova, A. van Strien, B. Huntley, Y. C. Collingham, D. Couvet, and R. E. Green. 2009. An Indicator of the Impact of Climatic Change on European Bird Populations. Plos One **4**.

Guisan, A. and W. Thuiller. 2005. Predicting species distribution: offering more than simple habitat models. Ecology Letters **8**:993-1009.

Guisan, A. and N. E. Zimmermann. 2000. Predictive habitat distribution models in ecology. Ecological Modelling **135**:147-186.

Hannaford, J., E. H. Pinn, and A. Diaz. 2006. The impact of sika deer grazing on the vegetation and infauna of Arne saltmarsh. Marine Pollution Bulletin **53**:56-62.

Harris, S., P. Morris, S. Wray, and D. Yalden. 1995. A review of British mammals: population estimates and conservation status of British mammals other than cetaceans. Joint Nature Conservation Committee.

Harrison, K. A. and R. D. Bardgett. 2004. Browsing by red deer negatively impacts on soil nitrogen availability in regenerating native forest. Soil Biology & Biochemistry **36**:115-126.

Heikkinen, R. K., M. Luoto, R. Virkkala, R. G. Pearson, and J.-H. Korber. 2007. Biotic interactions improve prediction of boreal bird distributions at macro-scales. Global Ecology and Biogeography **16**:754-763.

Hemami, M.-R., A. R. Watkinson, and P. M. Dolman. 2005. Population densities and habitat associations of introduced muntjac *Muntiacus reevesi* and native roe deer Capreolus capreolus in a lowland pine forest. Forest Ecology and Management **215**:224-238.

Hemami, M. R., A. R. Watkinson, and P. M. Dolman. 2004. Habitat selection by sympatric muntjac (*Muntiacus reevesi*) and roe deer (*Capreolus capreolus*) in a lowland commercial pine forest. Forest Ecology and Management **194**:49-60.

Hemami, M. R., A. R. Watkinson, R. M. A. Gill, and P. M. Dolman. 2007. Estimating abundance of introduced Chinese muntjac *Muntiacus reevesi* and native roe deer *Capreolus capreolus* using portable thermal imaging equipment. Mammal Review **37**:246-254.

Hester, A. J., L. Edenius, R. M. Buttenschon, and A. T. Kuiters. 2000. Interactions between forests and herbivores: the role of controlled grazing experiments. Forestry **73**:381-391.

Hester, A. J., I. J. Gordon, G. J. Baillie, and E. Tappin. 1999. Foraging behaviour of sheep and red deer within natural heather grass mosaics. Journal of Applied Ecology **36**:133-146.

Hewison, A. J. M. 1996. Variation in the fecundity of roe deer in Britain: Effects of age and body weight. Acta Theriologica **41**:187-198.

Hewison, A. J. M. and J. M. Gaillard. 1996. Birth-sex ratios and local resource competition in roe deer, *Capreolus capreolus*. Behavioral Ecology **7**:461-464.

Hewson, C. M., A. Amar, J. A. Lindsell, R. M. Thewlis, S. Butler, K. Smith, and R. J. Fuller. 2007. Recent changes in bird populations in British broadleaved woodland. Ibis **149**:14-28.

Hewson, C. M. and D. G. Noble. 2009. Population trends of breeding birds in British woodlands over a 32-year period: relationships with food, habitat use and migratory behaviour. Ibis **151**:464-486.

Hijmans, R. J. and C. H. Graham. 2006. The ability of climate envelope models to predict the effect of climate change on species distributions. Global Change Biology **12**:2272-2281.

Hill, J. K., C. D. Thomas, R. Fox, M. G. Telfer, S. G. Willis, J. Asher, and B. Huntley. 2002. Responses of butterflies to twentieth century climate warming: implications for future ranges. Proceedings of the Royal Society of London Series B-Biological Sciences **269**:2163-2171.

Holdo, R. M., J. M. Fryxell, A. R. E. Sinclair, A. Dobson, and R. D. Holt. 2011. Predicted impact of barriers to migration on the Serengeti wildebeest population. Plos One **6**:e16370.

Hole, D. G., S. G. Willis, D. J. Pain, L. D. Fishpool, S. H. M. Butchart, Y. C. Collingham, C. Rahbek, and B. Huntley. 2009. Projected impacts of climate change on a continent-wide protected area network. Ecology Letters **12**:420-431.

Holland, E. P., R. P. Pech, W. A. Ruscoe, J. P. Parkes, G. Nugent, and R. P. Duncan. 2013. Thresholds in plant-herbivore interactions: predicting plant mortality due to herbivore browse damage. Oecologia **172**:751-766.

Holloway, C. W. 1967. The effects of red deer and other animals on netural regeneration of Scots pine. University of Aberdeen.

Holmes, F. 1974. Following the roe. A natural history of the roe deer. J. Bartholomew.

Holt, C. A., R. J. Fuller, and P. M. Dolman. 2010. Experimental evidence that deer browsing reduces habitat suitability for breeding Common nightingale *Luscinia megarhynchos*. Ibis **152**:335 - 346.

Holt, C. A., R. J. Fuller, and P. M. Dolman. 2011. Breeding and post-breeding responses of woodland birds to modification of habitat structure by deer. Biological Conservation **144**:2151-2162.

Holt, R. D., S. W. Pacala, T. W. Smith, and J. G. Liu. 1995. Linking contemporary vegetation models with spatially explicit animal population models. Ecological Applications **5**:20-27.

Horsley, S. B., S. L. Stout, and D. S. DeCalesta. 2003. White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. Ecological Applications **13**:98-118.

Huntley, B., P. Barnard, R. Altwegg, L. Chambers, B. W. T. Coetzee, L. Gibson, P. A. R. Hockey, D. G. Hole, G. F. Midgely, L. G. Underhill, and S. G. Willis. 2010. Beyond bioclimatic

envelopes: dynamic species' range and abundance modelling in the context of climate change. Ecography **33**:621 - 626.

Huntley, B., Y. C. Collingham, S. G. Willis, and R. E. Green. 2008. Potential impacts of climatic change on European breeding birds. Plos One **3**.

Husheer, S. W., D. A. Coomes, and A. W. Robertson. 2003. Long-term influences of introduced deer on the composition and structure of New Zealand Nothofagus forests. Forest Ecology and Management **181**:99-117.

Iordan, F., S. P. Rushton, D. W. Macdonald, and L. Bonesi. 2012. Predicting the spread of feral populations of the American mink in Italy: is it too late for eradication? Biological Invasions **14**:1895-1908.

Irvine, R. J., M. Broadmeadow, R. M. A. Gill, and S. D. Albon. 2007. Deer and global warming: how will climate change influence deer populations? Deer **14**:34 - 37.

Irvine, R. J., S. Fiorini, S. Yearley, J. E. McLeod, A. Turner, H. Armstrong, P. C. L. White, and R. v. d. Wal. 2009. Can managers inform models? Integrating local knowledge into models of red deer habitat use. Journal of Applied Ecology **46**:344-352.

Jarman, P. J. 1974. Social organisiation of antelope in relation to their ecology. Behaviour **48**:215-&.

Jarnevich, C. S. and L. V. Reynolds. 2011. Challenges of predicting the potential distribution of a slow-spreading invader: a habitat suitability map for an invasive riparian tree. Biological Invasions **13**:153-163.

Jennings, B. 2009. A spatially explicit model of the white-tailed deer population in Delaware. M.Sc. University of Delaware.

Jepsen, B. I., H. R. Siegismund, and M. Fredholm. 2002. Population genetics of the native caribou (Rangifer tarandus groenlandicus) and the semi-domestic reindeer (Rangifer tarandus tarandus) in Southwestern Greenland: Evidence of introgression. Conservation Genetics **3**:401-409.

Jiguet, F., V. Devictor, R. Julliard, and D. Couvet. 2012. French citizens monitoring ordinary birds provide tools for conservation and ecological sciences. Acta Oecologica-International Journal of Ecology **44**:58-66.

Johnson, B. K., J. W. Kern, M. J. Wisdom, S. L. Findholt, and J. G. Kie. 2000. Resource selection and spatial separation of mule deer and elk during spring. Journal of Wildlife Management **64**:685-697.

Joys, A. C., R. J. Fuller, and P. M. Dolman. 2004. Influences of deer browsing, coppice history, and standard trees on the growth and development of vegetation structure in coppiced woods in lowland England. Forest Ecology and Management **202**:23-37.

Kay, S. 1993. Factors affecting severity of deer browsing damage within coppiced woodlands in the south of England. Biological Conservation **63**:217-222.

Kearney, M., B. L. Phillips, C. R. Tracy, K. A. Christian, G. Betts, and W. P. Porter. 2008. Modelling species distributions without using species distributions: the cane toad in Australia under current and future climates. Ecography **31**:423-434.

Kearney, M. and W. Porter. 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. Ecology Letters **12**:334-350.

Keith, D. A., H. R. Akcakaya, W. Thuiller, G. F. Midgley, R. G. Pearson, S. J. Phillips, H. M. Regan, M. B. Araujo, and T. G. Rebelo. 2008. Predicting extinction risks under climate change: coupling stochastic population models with dynamic bioclimatic habitat models. Biology Letters **4**:560-563.

Kerr, C. L. 2012. Range changes in British butterflies: the roles of climate, habitat and dispersal in patterns of spread. M.Sc.R. Durham University.

Kirby, K. J. 2001. The impact of deer on the ground flora of British broadleaved woodland. Forestry **74**:219-229.

Kleintjes Neff, P. K., S. M. Fettig, and D. R. VanOverbeke. 2007. Variable response of butterflies and vegetation to elk herbivory: an exclosure experiment in ponderosa pine and aspen-mixed conifer forests. Southwestern Naturalist **52**:1-14.

Langbein, J. 2011. Monitoring reported deer road casulaties and related accidents in England to 2010. The Deer Initiative, Research Report 2011/3.

Latham, J., B. W. Staines, and M. L. Gorman. 1999. Comparative feeding ecology of red (*Cervus elaphus*) and roe deer (*Capreolus capreolus*) in Scottish plantation forests. Journal of Zoology **247**:409-418.

Levinsky, I., F. Skov, J.-C. Svenning, and C. Rahbek. 2007. Potential impacts of climate change on the distributions and diversity patterns of European mammals. Biodiversity and Conservation **16**:3803-3816.

Lindenmayer, D. B. and R. C. Lacy. 1995. A simulation study of the impacts of population subdivision on the mountain brushtail possum *Trichosurus caninus* Ogilby (Phalangeridae: Marsupialia) in south-eastern Australia. I. Demographic stability and population persistence. Biological Conservation **73**:119-129.

Linkie, M., G. Chapron, D. J. Martyr, J. Holden, and N. Leader-Williams. 2006. Assessing the viability of tiger subpopulations in a fragmented landscape. Journal of Applied Ecology **43**:576-586.

Liu, C. R., P. M. Berry, T. P. Dawson, and R. G. Pearson. 2005. Selecting thresholds of occurrence in the prediction of species distributions. Ecography **28**:385-393.

Lopez-Alfaro, C., C. F. Estades, D. K. Aldridge, and R. M. A. Gill. 2012. Individual-based modeling as a decision tool for the conservation of the endangered huemul deer (*Hippocamelus bisulcus*) in southern Chile. Ecological Modelling **244**:104-116.

Lowe, V. P. W. 1966. Observations on the dispersal of red deer on Rhum. Symposium of the Zoological Society of London **18**:211-228.

Lowe, V. P. W. 1969. Population dynamics of red deer (*Cervus elaphus*) on Rhum. Journal of Animal Ecology **38**:425-&.

Lurz, P. W. W., S. P. Rushton, L. A. Wauters, S. Bertolino, I. Currado, P. Mazzoglio, and M. D. F. Shirley. 2001. Predicting grey squirrel expansion in North Italy: a spatially explicit modelling approach. Landscape Ecology **16**:407-420.

MacDonald, D. W. and P. J. Johnson. 2008. Sex ratio variation and mixed pairs in roe deer: evidence for control of sex allocation? Oecologia **158**:361-370.

Manel, S., J. M. Dias, S. T. Buckton, and S. J. Ormerod. 1999. Alternative methods for predicting species distribution: an illustration with Himalayan river birds. Journal of Applied Ecology **36**:734-747.

Mann, H. B. and D. R. Whitney. 1947. On a test of whether one of two random variables is stochasitcally larger than the other. Annals of Mathematical Statistics **18**:50-60.

Marshal, J. P., V. C. Bleich, and N. G. Andrew. 2008. Evidence for interspecific competition between feral ass *Equus asinus* and mountain sheep *Ovis canadensis* in a desert environment. Wildlife Biology **14**:228-236.

Martin, J. L. and M. Joron. 2003. Nest predation in forest birds: influence of predator type and predator's habitat quality. Oikos **102**:641-653.

Martin, T. G., P. Arcese, and N. Scheerder. 2010. Browsing down our natural heritage: Deer impacts on vegetation structure and songbird populations across an island archipelago. Biological Conservation **144**:459-469.

Marucco, F. and E. J. B. McIntire. 2010. Predicting spatio-temporal recolonization of large carnivore populations and livestock depredation risk: wolves in the Italian Alps. Journal of Applied Ecology **47**:789-798.

Mason, T. H. E., P. A. Stephens, S. G. Willis, R. Chirichella, M. Apollonio, and S. A. Richards. 2012. Intraseasonal Variation in Reproductive Effort: Young Males Finish Last. American Naturalist **180**:823-830.

Mayle, B. A. 1996. Progress in predictive management of deer populations in British woodlands. Forest Ecology and Management **88**:187-198.

Mayle, B. A. 1999. Managing Deer in the Countryside. Forestry Commission Practice Note 006.

McCarthy, M. A., M. A. Burgman, and S. Ferson. 1995. Sensitivity analysis for models of population viability. Biological Conservation **73**:93-100.

McMaster, G. S. and W. W. Wilhelm. 1997. Growing degree-days: one equation, two interpretations. Agricultural and Forest Meteorology **87**:291-300.

McShea, W. J. and J. H. Rappole. 1992. White-tailed deer as keystone species within forest habitats of Virginia. Virginia Journal of Science **43**:177-186.

McShea, W. J. and J. H. Rappole. 2000. Managing the abundance and diversity of breeding bird populations through manipulation of deer populations. Conservation Biology **14**:1161-1170.

McShea, W. J., H. B. Underwood, and J. H. Rappole. 1997. The science of overabundance: Deer ecology and population management. Smithsonian Books, Washington.

Medley, K. A. 2009. Niche shifts during the global invasion of the Asian tiger mosquito, *Aedes albopictus* Skuse (Culicidae), revealed by reciprocal distribution models. Global Ecology and Biogeography **19**:122-133.

Merow, C., N. LaFleur, J. A. Silander, Jr., A. M. Wilson, and M. Rubega. 2011. Developing dynamic mechanistic species distribution models: predicting bird-mediated spread of invasive plants across northeastern North America. American Naturalist **178**:30-43.

Midgley, G. F., G. O. Hughes, W. Thuiller, and A. G. Rebelo. 2006. Migration rate limitations on climate change-induced range shifts in Cape Proteaceae. Diversity and Distributions **12**:555-562.

Millett, J., A. J. Hester, P. Millard, and A. J. S. McDonald. 2006. How do different competing species influence the response of Betula pubescens Ehrh. to browsing? Basic and Applied Ecology **7**:123-132.

Mitchell, B. and D. McCowan. 1986. Performance and population dynamics in relation to management of red deer (*Cervus elaphus*) at Glenfeshie, Inverness-shire, Scotland. Biological Conservation **37**:237-267.

Mitchell, F. J. G. and K. J. Kirby. 1990. The impact of large herbivores on the conservation of semi-natural woods in the British uplands. Forestry **63**:333-353.

Moore, N. P., J. D. Hart, and S. D. Langton. 1999. Factors influencing browsing by fallow deer Dama dama in young broad-leaved plantations. Biological Conservation **87**:255-260.

Morecroft, M. D., M. E. Taylor, S. A. Ellwood, and S. A. Quinn. 2001. Impacts of deer herbivory on ground vegetation at Wytham Woods, central England. Forestry **74**:251-257.

Morellet, N., S. Champely, J. M. Gaillard, P. Ballon, and Y. Boscardin. 2001. The browsing index: new tool uses browsing pressure to monitor deer populations. Wildlife Society Bulletin **29**:1243-1252.

Moyes, K., D. H. Nussey, M. N. Clements, F. E. Guinness, A. Morris, S. Morris, J. M. Pemberton, L. E. B. Kruuk, and T. H. Clutton-Brock. 2011. Advancing breeding phenology in response to environmental change in a wild red deer population. Global Change Biology **17**:2455-2469.

Nagelkerke, N. J. D. 1991. A note on a general definition of the coefficient of determination. Biometrika **78**:691-692.

Naujokaitis-Lewis, I. R., J. M. R. Curtis, P. Arcese, and J. Rosenfeld. 2009. Sensitivity analyses of spatial population viability analysis models for species at risk and habitat conservation planning. Conservation Biology **23**:225-229.

Newson, S. E., A. Johnston, A. R. Renwick, S. R. Baillie, and R. J. Fuller. 2012. Modelling large-scale relationships between changes in woodland deer and bird populations. Journal of Applied Ecology **49**:278-286.

Newson, S. E. and D. G. Noble. 2006. The production of population trends for UK mammals using BBS mammal data: 1995-2004 update. BTO Research Report **428**:i.

Nilsen, E. B., J. M. Gaillard, R. Andersen, J. Odden, D. Delorme, G. van Laere, and J. D. C. Linnell. 2009. A slow life in hell or a fast life in heaven: demographic analyses of contrasting roe deer populations. Journal of Animal Ecology **78**:585-594.

Nudds, T. D. 1977. Quantifying the vegetative structure of wildlife cover. Wildlife Society Bulletin **5**:113-117.

Nuttle, T., T. E. Ristau, and A. A. Royo. 2014. Long-term biological legacies of herbivore density in a landscape-scale experiment: forest understoreys reflect past deer density treatments for at least 20 years. Journal of Ecology **102**:221-228.

P.O.S.T. 2009. Wild Deer. Parliamentary Office of Science and Technology, POSTnote 325.

Palmer, S. C. F., A. J. Hester, D. A. Elston, I. J. Gordon, and S. E. Hartley. 2003. The perils of having tasty neighbors: Grazing impacts of large herbivores at vegetation boundaries. Ecology **84**:2877-2890.

Palmer, S. C. F. and A. M. Truscott. 2003. Browsing by deer on naturally regenerating Scots pine (Pines sylvestris L.) and its effects on sapling growth. Forest Ecology and Management **182**:31-47.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology Evolution and Systematics **37**:637-669.

Pearce, J. L. and M. S. Boyce. 2006. Modelling distribution and abundance with presence-only data. Journal of Applied Ecology **43**:405-412.

Pearson, R. G., W. Thuiller, M. B. Araujo, E. Martinez-Meyer, L. Brotons, C. McClean, L. Miles, P. Segurado, T. P. Dawson, and D. C. Lees. 2006. Model-based uncertainty in species range prediction. Journal of Biogeography **33**:1704-1711.

Perez-Espona, S., J. M. Pemberton, and R. Putman. 2009. Red and sika deer in the British Isles, current management issues and management policy. Mammalian Biology **74**:247-262.

Perrins, C. M. and R. Overall. 2001. Effect of increasing numbers of deer on bird populations in Wytham Woods, central England. Forestry **74**:299-309.

Peterson, A. T., M. Papes, and D. A. Kluza. 2003. Predicting the potential invasive distributions of four alien plant species in North America. Weed Science **51**:863-868.

Pettorelli, N., J. M. Gaillard, P. Duncan, D. Maillard, G. Van Laere, and D. Delorme. 2003. Age and density modify the effects of habitat quality on survival and movements of roe deer. Ecology **84**:3307-3316.

Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. Ecological Modelling **190**:231-259.

Pietz, P. J. and D. A. Granfors. 2000. White-tailed deer (Odocoileus virginianus) predation on grassland songbird nestlings. American Midland Naturalist **144**:419-422.

Pollard, E. and A. S. Cooke. 1994. Impact of muntjac deer *Muntiacus reevesi* on egg-laying sites of the white admiral butterfly *Ladoga camilla* in a Cambridgeshire wood. Biological Conservation **70**:189-191.

Pompilio, L. and A. Meriggi. 2001. Modelling wild ungulate distribution in Alpine habitat: a case study. Italian Journal of Zoology **68**:281-289.

Prentice, I. C., W. Cramer, S. P. Harrison, R. Leemans, R. A. Monserud, and A. M. Solomon. 1992. A global biome model based on plant physiology and dominance, soil properties and climate. Journal of Biogeography **19**:117-134.

Prior, R. 1995. The Roe Deer: Conservation of a Native Species. Swan Hill Press, U.K.

Pulliam, H. R., J. B. Dunning, and J. G. Liu. 1992. Population dynamics in complex landscapes: a case study. Ecological Applications **2**:165-177.

Putman, R., J. Langbein, P. Green, and P. Watson. 2011a. Identifying threshold densities for wild deer in the UK above which negative impacts may occur. Mammal Review **41**:175-196.

Putman, R., Langbein, J. 2003. The Deer Manager's Companion. Swan Hill Press.

Putman, R., P. Watson, and J. Langbein. 2011b. Assessing deer densities and impacts at the appropriate level for management: a review of methodologies for use beyond the site scale. Mammal Review **41**:197-219.

Putman, R. J. 1988. The natural history of deer. Comstock Publishing Associates.

Putman, R. J., P. J. Edwards, J. C. E. Mann, R. C. How, and S. D. Hill. 1989. Vegetational and faunal changes in an area of heavily grazed woodland following relief of grazing. Biological Conservation **47**:13-32.

Putman, R. J., J. Langbein, A. J. M. Hewison, and S. K. Sharma. 1996. Relative roles of density-dependent and density-independent factors in population dynamics of British deer. Mammal Review **26**:81-101.

Putman, R. J. and N. P. Moore. 1998. Impact of deer in lowland Britain on agriculture, forestry and conservation habitats. Mammal Review **28**:141-163.

R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Radeloff, V. C., A. M. Pidgeon, and P. Hostert. 1999. Habitat and population modelling of roe deer using an interactive geographic information system. Ecological Modelling **114**:287-304.

Rasband, W. S. 2010. ImageJ. United States National Institutes of Health, Bethesda, Maryland, U.S.A.

Ratcliffe, P. R. 1987. Distribution and current status of sika deer, Cervus nippon, in Great Britain. Mammal Review **17**:39-58.

Ratcliffe, P. R. 1989. The Control of Red and Sika Deer Populations in Commercial Forests. Pages 98 - 115 *in* R. Putman, editor. Mammals as Pests. Chapman & Hall, London.

Revilla, E. and T. Wiegand. 2008. Individual movement behavior, matrix heterogeneity, and the dynamics of spatially structured populations. Proceedings of the National Academy of Sciences **105**:19120-19125.

Richard, E., J.-M. Gaillard, S. Said, J.-L. Hamann, and F. Klein. 2010. High red deer density depresses body mass of roe deer fawns. Oecologia **163**:91-97.

Richards, S. A., M. J. Whittingham, and P. A. Stephens. 2011. Model selection and model averaging in behavioural ecology: the utility of the IT-AIC framework. Behavioral Ecology and Sociobiology **65**:77-89.

Richardson, D. M. and W. Thuiller. 2007. Home away from home - objective mapping of high-risk source areas for plant introductions. Diversity and Distributions **13**:299-312.

Ripple, W. J. and R. L. Beschta. 2012. Trophic cascades in Yellowstone: The first 15 years after wolf reintroduction. Biological Conservation **145**:205-213.

Robinson, R. A. 2005. BirdFacts: profiles of birds occurring in Britain & Ireland (BTO Research Report). British Trust for Ornithology, Thetford.

Robinson, R. A., S. R. Baillie, and H. Q. P. Crick. 2007. Weather-dependent survival: implications of climate change for passerine population processes. Ibis **149**:357-364.

Rooney, T. P. and D. M. Waller. 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. Forest Ecology and Management **181**:165-176.

Root, T. L., J. T. Price, K. R. Hall, S. H. Schneider, C. Rosenzweig, and J. A. Pounds. 2003. Fingerprints of global warming on wild animals and plants. Nature **421**:57-60.

Rossell, C. R., B. Gorsira, and S. Patch. 2005. Effects of white-tailed deer on vegetation structure and woody seedling composition in three forest types on the Piedmont Plateau. Forest Ecology and Management **210**:415-424.

Ruckelshaus, M., C. Hartway, and P. Kareiva. 1997. Assessing the data requirements of spatially explicit dispersal models. Conservation Biology **11**:1298-1306.

Rushton, S., R. Sanderson, M. Luff, and R. Fuller. 1996. Modelling the spatial dynamics of ground beetles (Carabidae) within landscapes. Annales Zoologici Fennici **33**:233-241.

Rushton, S. P., P. W. W. Lurz, R. Fuller, and P. J. Garson. 1997. Modelling the distribution of the red and grey squirrel at the landscape scale: a combined GIS and population dynamics approach. Journal of Applied Ecology **34**:1137-1154.

Sage, R. B., K. Hollins, C. L. Gregory, M. I. A. Woodburn, and J. P. Carroll. 2004. Impact of roe deer *Capreolus capreolus* browsing on understorey vegetation in small farm woodlands. Wildlife Biology **10**:115-120.

Scott, D., D. Welch, and D. A. Elston. 2009. Long-term effects of leader browsing by deer on the growth of Sitka spruce (Picea sitchensis). Forestry **82**:387-401.

Senn, H. V., N. H. Barton, S. J. Goodman, G. M. Swanson, K. A. Abernethy, and J. M. Pemberton. 2010. Investigating temporal changes in hybridization and introgression in a predominantly bimodal hybridizing population of invasive sika (Cervus nippon) and native red deer (C-elaphus) on the Kintyre Peninsula, Scotland. Molecular Ecology **19**:910-924.

Simas, A. B., W. Barreto-Souza, and A. V. Rocha. 2010. Improved estimators for a general class of beta regression models. Computational Statistics & Data Analysis **54**:348-366.

Simberloff, D. 1998. Flagships, umbrellas, and keystones: Is single-species management passe in the landscape era? Biological Conservation **83**:247-257.

Skaug, H., D. Fournier, A. Nielsen, A. Magnusson, and B. Bolker. 2011. glmmADMB: Generalized Linear Mixed Models Using AD Model Builder. R package version 0.7.1/r171; http://R-Forge.R-project.org/projects/glmmadmb/

Smith, R. L. and T. M. Smith. 2001. Ecology and field biology. Benjamin Cummings, USA.

South, A. 1999. Dispersal in spatially explicit population models. Conservation Biology **13**:1039-1046.

Staines, B., S. C. F. Palmer, I. Wyllie, R. M. A. Gill, and B. A. Mayle. 1998. Desk and limited field studies to analyse the major factors influencing regional deer populations and ranging behaviour. Institute of Terrestrial Ecology (Natural Environment Research Council).

Staines, B. W. 1974. A review of factors affecting deer dispersion and their relevance to management Mammal Review **4**:79-91.

Staines, B. W. and P. R. Ratcliffe. 1987. Estimating the abundance of red deer (Cervus elaphus L.) and roe deer (Capreolus capreolus L.) and their current status in Great Britain. Pages 131 - 152 Symposia of the Zoological Society of London.

Stewart, A. J. A. 2001. The impact of deer on lowland woodland invertebrates: a review of the evidence and priorities for future research. Forestry **74**:259-270.

Stone, J., P. M. Dolman, and R. J. Fuller. 2004. Impacts of deer grazing on regenerating coppice stools and ground flora: an exclosure study in Bradfield Woods, England. Quarterly Journal of Forestry **93**:257 - 262.

Sutherland, W. J. 2006. Ecological Census Techniques: A Handbook, 2nd Edition.

Tanentzap, A. J., D. R. Bazely, S. Koh, M. Timciska, E. G. Haggith, T. J. Carleton, and D. A. Coomes. 2011. Seeing the forest for the deer: Do reductions in deer-disturbance lead to forest recovery? Biological Conservation **144**:376-382.

Tanentzap, A. J., L. E. Burrows, W. G. Lee, G. Nugent, J. M. Maxwell, and D. A. Coomes. 2009. Landscape-level vegetation recovery from herbivory: progress after four decades of invasive red deer control. Journal of Applied Ecology **46**:1064-1072.

Tanentzap, A. J., J. Zou, and D. A. Coomes. 2013. Getting the biggest birch for the bang: restoring and expanding upland birchwoods in the Scottish Highlands by managing red deer. Ecology and Evolution **3**:1890 - 1901.

The Deer Initiative. 2007. Deer on our Roads - Counting the Cost. The Deer Initiative.

The Deer Initiative. 2008. Species ecology: red deer (http://www.thedeerinitiative.co.uk/uploads/guides/168.pdf). England and Wales Best Practice Guides.

Thuiller, W., O. Broennimann, G. Hughes, J. R. M. Alkemade, G. F. Midgley, and F. Corsi. 2006a. Vulnerability of African mammals to anthropogenic climate change under conservative land transformation assumptions. Global Change Biology **12**:424-440.

Thuiller, W., S. Lavorel, M. T. Sykes, and M. B. Araujo. 2006b. Using niche-based modelling to assess the impact of climate change on tree functional diversity in Europe. Diversity and Distributions **12**:49-60.

Travis, J. M. J., C. M. Harris, K. J. Park, and J. M. Bullock. 2011. Improving prediction and management of range expansions by combining analytical and individual-based modelling approaches. Methods in Ecology and Evolution **2**:477-488.

Travis, J. M. J., K. Mustin, K. A. Barton, T. G. Benton, J. Clobert, M. M. Delgado, C. Dytham, T. Hovestadt, S. C. F. Palmer, H. Van Dyck, and D. Bonte. 2012. Modelling dispersal: an eco-evolutionary framework incorporating emigration, movement, settlement behaviour and the multiple costs involved. Methods in Ecology and Evolution **3**:628-641.

Urban, M. C., B. L. Phillips, D. K. Skelly, and R. Shine. 2007. The cane toad's (Chaunus [Bufo] marinus) increasing ability to invade Australia is revealed by a dynamically updated range model. Proceedings of the Royal Society B-Biological Sciences **274**:1413-1419.

Urbanek, S. 2012. png: read and write PNG images. R package version 0.1-4.*in* www.rforge.net/png, editor.

van Beurden, E. 1981. Bioclimatic limits to the spread of Bufo marinus in Australia: a baseline. Proceedings of the Ecological Society of Australia **11**:143-149.

Van Moorter, B., J. M. Gaillard, A. J. M. Hewison, S. Said, A. Coulon, D. Delorme, O. Widmer, B. Cargnelutti, and J. M. Angibault. 2008. Evidence for exploration behaviour in young roe deer (Capreolus capreolus) prior to dispersal. Ethology Ecology & Evolution **20**:1-15.

Vanhinsbergh, D., R. J. Fuller, and D. Noble. 2001. An analysis of changes in the populations of British woodland birds and a review of possible causes. British Trust for Ornithology.

Vila , M., C. Basnou, P. PyÅ¡ek, M. Josefsson, P. Genovesi, S. Gollasch, W. Nentwig, S. Olenin, A. Roques, D. Roy, and P. E. Hulme. 2009. How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. Frontiers in Ecology and the Environment **8**:135-144.

Wäber, K. 2010. Landscape scale deer management. Ph.D. University of East Anglia.

Wäber, K., J. Spencer, and P. M. Dolman. 2013. Achieving landscape-scale deer management for biodiversity conservation: The need to consider sources and sinks. The Journal of Wildlife Management **77**:726 - 736.

Wahlstrom, L. K. and O. Liberg. 1995. Patterns of dispersal and seasonal migration in roe deer (Capreolus capreolus). Journal of Zoology **235**:455-467.

Waller, D. M. and W. S. Alverson. 1997. The white-tailed deer: a keystone herbivore. Wildlife Society Bulletin **25**:217-226.

Ward, A., T. Etherington, and J. Ewald. 2008. Five years of change. Deer **14**:17-20.

Ward, A. I. 2001. The ecology and sustainable management of roe deer (*Capreolus capreolus*) in multiple-use forestry. University of York.

Ward, A. I. 2005. Expanding ranges of wild and feral deer in Great Britain. Mammal Review **35**:165-173.

Ward, A. I. and K. Lees. 2011. Analysis of cost of preventing establishment in Scotland of muntjac deer *(Muntiacus spp.*). Scottish Natural Heritage Commissioned Report No. 457.

Wardle, D. A. and R. D. Bardgett. 2004. Human-induced changes in large herbivorous mammal density: the consequences for decomposers. Frontiers in Ecology and the Environment **2**:145-153.

Wauters, L. A., S. A. Decrombrugghe, N. Nour, and E. Matthysen. 1995. Do female roe deer in good condition produce more sons than daughters. Behavioral Ecology and Sociobiology **37**:189-193.

Weisberg, P. J., N. T. Hobbs, J. E. Ellis, and M. B. Coughenour. 2002. An ecosystem approach to population management of ungulates. Journal of Environmental Management **65**:181-197.

Welch, D., B. W. Staines, D. Scott, and D. D. French. 1992. Leader browsing by red and roe deer on young sitka spruce trees in western Scotland. 2. Effects on growth and tree form. Forestry **65**:309-330.

Welch, D., B. W. Staines, D. Scott, D. D. French, and D. C. Catt. 1991. Leader browsing by red and roe deer on young sitka spruce trees in western Scotland. 1. Damage rates and the influence of habitat factors. Forestry **64**:61-82.

White, M. A. 2012. Long-term effects of deer browsing: Composition, structure and productivity in a northeastern Minnesota old-growth forest. Forest Ecology and Management **269**:222-228.

Whitehead, G. K. 1964. The deer of Great Britain and Ireland. An account of their history, status and distribution. The deer of Great Britain and Ireland. An account of their history, status and distribution.:pp. xv, 597.

Wiegand, T., F. Knauer, P. Kaczensky, and J. Naves. 2004a. Expansion of brown bears (Ursus arctos) into the eastern Alps: a spatially explicit population model. Biodiversity and Conservation **13**:79-114.

Wiegand, T., E. Revilla, and F. Knauer. 2004b. Dealing with uncertainty in spatially explicit population models. Biodiversity and Conservation **13**:53 - 78.

Wilcox, R. B., J. D. Brotherson, and W. E. Evenson. 1981. Canopy influence on understory community composition. Northwest Science **55**:194 - 201.

Willis, S. G., C. D. Thomas, J. K. Hill, Y. C. Collingham, M. G. Telfer, R. Fox, and B. Huntley. 2009. Dynamic distribution modelling: predicting the present from the past. Ecography **32**:5-12.

Yalden, D. 1999. The history of British Mammals. Academic Press Inc.

Zalba, S. M. and N. C. Cozzani. 2004. The impact of feral horses on grassland bird communities in Argentina. Animal Conservation **7**:35-44.

Zurell, D., F. Jeltsch, C. F. Dormann, and B. Schroder. 2009. Static species distribution models in dynamically changing systems: how good can predictions really be? Ecography **32**:733-744.

Appendices

Appendix 1. Model selection results for models describing habitat suitability for roe, red and muntjac deer.

Table S1. The confidence set (models within six Δ AIC units of the AIC best model, and lower Δ AIC than simpler nested models, following Richards *et al.* (2011)) for models to predict habitat suitability across Britain for roe deer, red deer, and Reeves' muntjac deer, sorted by lowest Δ AIC. For the presence-only approach, the AUC best model for each species is provided. Variable codes refer to those provided in Table 2-2.

Species	Modelling approach	Model Ref.	Fixed variables	Δ AIC (AUC)
Roe	Abundance	1	C1+C2+C3+C4+C6+C7+C2*C4	0.0
		2	C1+C2+C3+C4+C6+C7+C2*C3	2.0
		3	C1+C2+C3+C4+C5+C6+C2*C4	2.2
		4	C1+C2+C3+C4+C5+C6+C8+C2*C4	3.6
		5	C1+C2+C3+C4+C5+C6+C2*C3	4.4
		6	C1+C2+C3+C4+C6+C7+C2*C4	5.6
	Presence/absence	7	C1+C2+C3+C4+C5+C6+C3*C6	0.0
		8	C1+C2+C3+C4+C6+C3*C6	1.2
	Presence only	9	C2+C3+C6	(0.62)
Muntjac	Abundance	1	C1+C2+C3+C5+C6+C8+C2*C3	0.0
		2	C2+C3+C4+C5+C6+C7+C8+C2*C3	1.1
		3	C1+C2+C3+C4+C6+C7+C8+C2*C3	1.3
		4	C1+C2+C3+C5+C6+C2*C3	3.7
		5	C1+C2+C3+C4+C5+C7+C2*C3	4.0
		6	C1+C2+C3+C6+C8+C2*C3	4.3
	Presence/absence	7	C1+C2+C3+C4+C5+C6+C7+C8+C3*C5	0.0
		8	C1+C2+C3+C4+C5+C6+C7+C3*C5	0.3
		9	C1+C3+C4+C5+C6+C7+C8+C3*C5	0.4
		10	C1+C3+C4+C5+C6+C7+C3*C5	0.4
		11	C1+C2+C3+C5+C6+C7+C3*C5	0.7
		12	C1+C3+C5+C6+C7+C3*C5	1.6
	Presence only	13	C1+C3+C6+C7	(0.78)
Red	Abundance	1	C1+C2+C5+C6+C7+C1*C5	0.0
		2	C1+C2+C3+C4+C5+C6+C1*C5	3.9
		3	C1+C3+C5+C6+C7+C1*C5	3.9
		4	C1+C2+C4+C5+C6+C1*C5	5.4
		5	C1+C2+C5+C6+C1*C5	5.6
	Presence/absence	6	C1+C2+C3+C4+C5+C6+C7+C8+C2*C5	0.0
		7	C1+C2+C3+C4+C5+C6+C7+C8+C4*C6	1.4
		8	C2+C3+C4+C5+C6+C7+C8+C2*C5	1.4
		9	C1+C2+C3+C4+C6+C7+C8+C4*C6	1.8
		10	C2+C3+C5+C6+C7+C8+C2*C5	1.8
		11	C1+C2+C3+C4+C6+C7+C4*C6	5.0
	Presence only	12	C2+C3+C4+C6+C8	(0.71)

Appendix 2. Species-specific parameter estimates for population models, obtained from the literature

Density of deer in prime habitats

Density of roe deer in prime habitats

Estimates of approximately 25 deer per km^{-2} have been reported in Scottish woodlands (Mayle 1996) and pine forests in East Anglia (Hemami et al. 2005), and 13 deer km^{-2} in mixed woodland in Hampshire (see Harris et al. 1995). Populations of approximately 10 deer km^{-2} are most common, but densities can reach up to 30 km^{-2} in some areas (Staines and Ratcliffe 1987, Ward 2001). An extremely high estimate (up to 75 roe deer km^{-2}) was recorded in isolated woodlands in southern England, however, this was thought to be an overestimate given that those woodlands only incorporated part of the species' home range (Loudon 1982, in Harris et al. 1995).

Density of red deer in prime habitats

In good quality woodland habitats, densities of up to 40 red deer km^{-2} have been reported (Harris et al. 1995, Staines et al. 1998). In open hill habitats, similar densities are found across the year (Staines & Balharry, in Staines *et al.* 1998). However, Harris *et al.* (1995) report that densities of red deer in upland areas are typically lower, in the region of 12 to 15 km^{-2}.

Density of muntjac deer in prime habitats

While densities of up to 120 muntjac deer per km^2 were recorded in Monks Wood, Cambridgeshire, in 1994, this was classed as 'unusually high' and the population subsequently more than halved the following year, reaching densities of approximately 57 deer km^{-2} (Cooke et al. 1996). More commonly, maximum densities of approximately 30 deer km^{-2} (Chapman et al. 1995 in Hemami et al. 2005; Wäber et al. 2013; Wyllie et al. in Staines et al. 1998). Therefore, for the purpose of this chapter, maximum density in prime habitat was set at 30 deer km^{-2}; this value was used by Harris *et al.* (1995) when creating population estimates for muntjac deer in Britain.

In Britain, populations of roe, red and muntjac deer are female biased; red deer populations contain approximately twice as many females as males (adult sex ratio is therefore 0.33) (Clutton-Brock et al. 2002), and roe and muntjac deer populations contain approximately 63% and 62% females, respectively (Wäber et al. 2013). The adult sex ratio was therefore 0.37 and 0.38, respectively) (Wäber et al. 2013). ***MaxK*** for red, roe and muntjac deer were adjusted by multiplying the maximum density of each species by their adult sex ratios. Therefore, for roe, muntjac and red deer, ***MaxK*** was set to 19, 19 and 27, respectively.

Demographic parameters

Litter size and probability of breeding

Roe deer litter size and probability of breeding

In a study of 15 roe deer populations in Britain, Hewison (1996) found that the majority of yearlings reproduced successfully, but that the number of offspring they produced was lower than that of adults; mean pregnancy rates for yearlings and adults were 0.81 (min = 0.67; max = 0.94) and 0.66 (min = 0.35; max = 1.00), respectively. Therefore, I set the age of first breeding (***AgeFirstBreed***) to 1, but varied the probability of breeding according to age class. The probability of adult- (***pBreedAdult***) and juvenile- (***pBreedJuvenile***) breeding was set to the mean values of 0.81 and 0.66, respectively.

In a study of roe deer in 41 sites across the UK, 72% of pregnancies produced twins, 27% singletons, and 1% triplets (MacDonald and Johnson 2008). The proportion of singleton, twin and triplet pregnancies were therefore set to 0.27, 0.72 and 0.01, respectively. Subsequently, the number of offspring was adjusted according to sex ratio of singletons, twins and triplets, which were set at 0.60, 0.51, and 0.50, respectively (based on MacDonald and Johnson 2008).

Muntjac deer litter size and probability of breeding

Virtually all females over two years of age become pregnant each year (***pBreedAdult*** = 1) while approximately 60% of juvenile females in British populations fall pregnant in any year (***pBreedJuvenile*** = 0.60) (Harris et al. 1995, Chapman et al. 1997). Muntjac

deer produce singleton offspring (Harris et al. 1995, Chapman et al. 1997, Wäber et al. 2013). Therefore, probability of singleton birth was set to 1. As I am modelling females only, I reduced the number of offspring according to the sex ratio at birth of 0.5 (Corbet and Harris 1991, Harris et al. 1995, Chapman et al. 1997).

The mean interval between births is 233 ± 3 days i.e. approximately every eight months (Chapman et al. 1997); therefore, the model was run using 8-month time steps. As muntjac females start breeding at approximately 7 months of age (Corbet and Harris 1991, Chapman et al. 1997, British Deer Society 2010c), the age at first breeding (***AgeFirstBreed***) was set to 1.

Red deer litter size and probability of breeding

Pregnancy rates of red deer are highly variable, with populations in lowlands generally being more productive than those in the highlands (Staines et al. 1998). There is also variability in pregnancy rates between years in the same sites, in response to population density and climate (Clutton-Brock and Coulson 2002). For example, in studies of red deer populations on the Isle of Rum, Scotland between 1957 and 1966 (Lowe 1969), and between 1985 and 2001 (Clutton-Brock and Coulson 2002), the proportion of 2-year-old calves which were pregnant were reported to be approximately 0.42 and 0.25, respectively (***AgeFirstBreed*** was therefore set to 2). In studies of red deer populations in seven Scottish woodland sites, the fertility of adult red deer ranged between 60% and 100%, and pregnancy rates of juveniles ranged from 0% to over 80% (Mayle 1996). Similarly, Clutton-Brock & Coulson (2002) found that pregnancy rates of red deer hinds on Rum were in the region of 0.60 – 0.95. In lowland populations, pregnancy rates of juveniles have been reported to be 65% yearlings and 100% adults pregnant; other places between 72 and 100% yearlings and 89 – 100% adults pregnant (Staines et al. 1998).

For the baseline models I used mean pregnancy rates of 0.9 for adults (The Deer Initiative 2008), and 0.5 for juveniles (from the values described in the paragraph above). Red deer hinds produce single offspring (Lowe 1969, Mitchell and McCowan 1986, Corbet and Harris 1991, Bonenfant et al. 2002, Clutton-Brock and Coulson 2002).

Number of offspring was subsequently adjusted according to the sex ratio at birth, which was has been observed to be 0.55 (Clutton-Brock and Lonergan 1994).

Survival rates

Roe deer survival rates

High natural mortality occurs within the first six months of life (British Deer Society 2010e) and fawn survival is very variable, ranging between 0.20 and 1.00 (Gill 1994). For example, in six locations in the U.K. (Pickering, Alice Holt, Thetford, Kershope, Spadeham, Craigellaichie), fawn survival was reported as ranging between 0.25 and 0.71 (Mayle 1996). However, a recent estimate of mean fawn survival rate of 0.83 for populations in Thetford Forest, Norfolk was reported (Wäber et al. 2013), which is significantly higher than the range of estimates (0.52 – 0.64) from the same location provided by Mayle (1996).

Adult survival rates tend to be less variable than fawn survival rates, as adults are less sensitive to factors such as severe winter weather conditions (Gaillard et al. 1993, Mayle 1996). Cobben *et al.* (2009), found that survival rates in a Norwegian population ranged between 0.91 and 1.00. This range of values encompasses a mean survival estimate of 0.95 reported in a Scottish population at Glen Righ, Inverness-shire (Mayle 1996), and from two populations in France (Gaillard et al. 1993). For the purposes of this chapter, I use a kid survival rate of 0.83 (Wäber et al. 2013), and a mean adult survival of 0.95 (Mayle 1996) in the baseline models.

Muntjac deer survival rates

The maximum life span of adult muntjac deer females has been reported as 19 years (Corbet and Harris 1991), which accords with an annual adult survival rate of approximately 0.8. The annual survival rate of juvenile muntjac deer recorded in a wild population in Thetford Forest, Norfolk was 0.65 (Wäber et al. 2013).

I accounted for the eight-month reproductive cycle in the estimates of survival, converting annual survival rates to eight-month survival rates, using equation 7-a:

$$\text{Survival} = \mathrm{T}^{g/12} \qquad \textbf{Equation 7-a}$$

where T is the annual survival rate, and gis the inter-birth interval, in months.

Consequently, estimates of adult survival (***SurvA***) and juvenile survival (***SurvJ***) used in the model were 0.86 and 0.75, respectively.

Red deer survival rates

Variation in red deer survival rates is high. One study of red deer on the Isle of Rum between 1973 and 1982 reported probabilities of female calf mortality between 0 and 0.55, and adult mortality between 0 and approximately 0.20 (Figures 2c and d in Albon et al. 1987, Clutton-Brock et al. 2002). These equate to calf survival rates between 0.45 and 1.00, and adult survival rates between 0.80 and 1.00. Mean survival rates for adults (SurvA = 0.95; Mayle 1996) and juveniles were used in the baseline models (SurvJ = 0.69; Coulson et al. 1997).

Dispersal

Roe deer dispersal

Yearlings disperse from natal areas when they are approximately one year old; after this, most individuals are very sedentary (Pettorelli et al. 2003, Gaillard et al. 2008, Van Moorter et al. 2008), with the exception of a small subset of individuals which undertake long-distance dispersal (Danilkin and Hewison 1996). Individuals usually disperse less than 2km from their natal ranges, however, distances of up to 20km have been recorded (Staines et al. 1998). The maximum possible dispersal steps (***DispersalSteps***) was set to 20.

Only two studies have explicitly reported a value for the probability of individuals undergoing pre-saturation dispersal in their SEPMs (Lindenmayer and Lacy 1995, South 1999); the former used a maximum value of 0.05 in their models of the spread of the mountain brushtail possum *Trichosurus caninus*, and the latter also used a value of 0.05 in their theoretical study. As roe deer dispersal rates are low (Wahlstrom and Liberg 1995), and they also undergo pre-saturation dispersal in response to habitat heterogeneities (Gaillard et al. 2008), I used the two studies described above as a guide and set ***pOptDisp*** to 0.05.

Muntjac deer dispersal

There are very few published estimates of dispersal in muntjac deer, although theoretical studies have shown they are able to disperse relatively easily, even in fragmented habitats (Angold et al. 2006). While the majority of individuals have been recorded within 4km of their natal range, some have been recorded to move up to 13km (Chapman et al. 1994). Therefore, the maximum number of dispersal steps was set to 13 (***DispersalSteps*** = 13) in the models. Muntjac deer, like the roe deer, undergo pre-saturation dispersal, and therefore ***pOptDisp*** was set to 0.05 for this species (see justification in: *Roe deer dispersal*).

Red deer dispersal

The large-bodied British deer species (red, fallow and sika) are termed saturation dispersers, showing little movement away from natal ranges until very high local densities are reached (Corbet and Harris 1991, Clutton-Brock et al. 2002, Ward 2005). Consequently, probability of optional dispersal (***pOptDisp***: the proportion of individuals which disperse when density is below the carrying capacity) was set to a nominal value of 0.01 (see Figure 2e in Clutton-Brock et al. 2002).

Most female red deer remain in the vicinity of where they were born (Lowe 1966, Staines 1974, Corbet and Harris 1991, Clutton-Brock and Coulson 2002). Mean dispersal distances obtained from calf-tagging programmes on estates in Scotland were in the order of 3km for females and 5km for males (Daniels and McClean 2003). In addition, Daniels & McClean (2003) found that maximum dispersal distances were 31km for hinds, and 58km for stags. As I am modelling females only, the maximum possible dispersal steps (***DispersalSteps***) was set to 31.

Appendix 3. Temporal trends in deer abundance in my field sites

Generalised linear models with a poisson error distribution were used to determine if temporal trends in deer abundance were stable, increasing or decreasing over time in each of my field sites. Deer counts were the response variable, and year the predictor variable. I found that deer counts in each site were stable over time (as demonstrated by the non-significant *p* values in Table S 2).

Table S 2. Parameter values from generalised linear models with poisson error distributions, used to determine if temporal trends in deer abundance were stable, increasing or decreasing over time. Roe is the mean number of roe deer recorded by Breeding Bird Survey volunteers across all years' survey, per site. *p* denotes the significance of the *Z*-tests.

BBS Ref.	Grid Ref.	Easting	Northing	No. Years	Roe	Est.	*Z*	*p*
620	SD8211	382000	411000	15	0.00	0	0	1
671	SE4629	446000	429000	10	0.00	0	0	1
814	SO7472	374000	272000	14	0.00	0	0	1
819	SO8152	381000	252000	15	0.00	0	0	1
886	SP2528	425000	228000	4	0.00	0	0	1
1470	SU9267	492000	167000	10	0.00	0	0	1
1503	SX2453	224000	53000	5	0.00	0	0	1
1987	TQ1829	518000	129000	5	0.00	0	0	1
2060	TQ5460	554000	160000	15	0.00	0	0	1
1943	TQ0146	501000	146000	15	0.57	0.15	1.67	0.10
822	SO8711	387000	211000	4	0.75	0.42	0.76	0.45
1157	ST7879	378000	179000	14	0.77	0.09	1.11	0.27
1516	SX5997	259000	97000	11	0.80	-0.01	-0.12	0.91
628	SD8815	388000	415000	14	0.83	0.16	1.58	0.11
1044	ST3406	334000	106000	4	1.25	-0.62	-1.33	0.18
1410	SU7225	472000	125000	4	1.25	0.24	0.6	0.55
523	NZ0651	406000	551000	9	1.38	0.09	0.95	0.34
1180	ST8603	386000	103000	10	1.44	0.01	0.22	0.82
1469	SU9240	492000	140000	16	1.64	-0.04	-0.88	0.38
1069	ST4766	347000	166000	12	1.90	-0.05	-1.07	0.29
1420	SU7653	476000	153000	15	2.14	0.06	1.53	0.12
1263	SU3020	430000	120000	16	2.20	0.05	1.27	0.21
1047	ST3624	336000	124000	3	3.00	0.34	0.81	0.42
1300	SU4364	443000	164000	4	3.00	0.07	0.26	0.80
1550	SY3597	335000	97000	10	3.00	-0.01	-0.32	0.75
1369	SU6112	461000	112000	13	3.15	0.05	1.19	0.23
1084	ST5472	354000	172000	12	3.17	-0.08	-0.74	0.46
1224	SU0811	408000	111000	14	3.54	-0.01	-0.2	0.84
1402	SU6928	469000	128000	4	4.00	0.15	0.67	0.50
634	SD9243	392000	443000	15	4.14	0.03	0.85	0.40
1217	SU0514	405000	114000	15	4.21	-0.01	-0.20	0.84
1216	SU0486	404000	186000	12	4.75	-0.28	-1.32	0.19
1244	SU2143	421000	143000	9	5.33	0.07	1.48	0.14
1203	ST9809	398000	109000	13	5.92	0.00	0.14	0.89
1396	SU6725	467000	125000	3	6.00	0.08	0.29	0.77

Appendix 4.

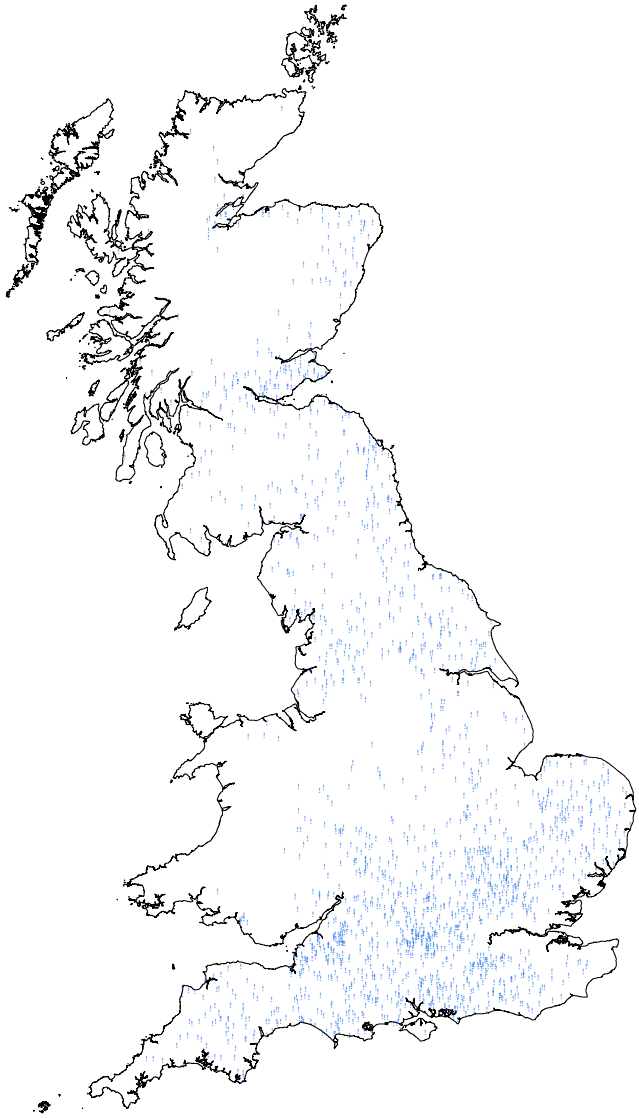


Figure S 1. Location of breeding bird survey sites used in the analysis in Chapter 6. Each blue dot represents the location of a 1km^2 site.

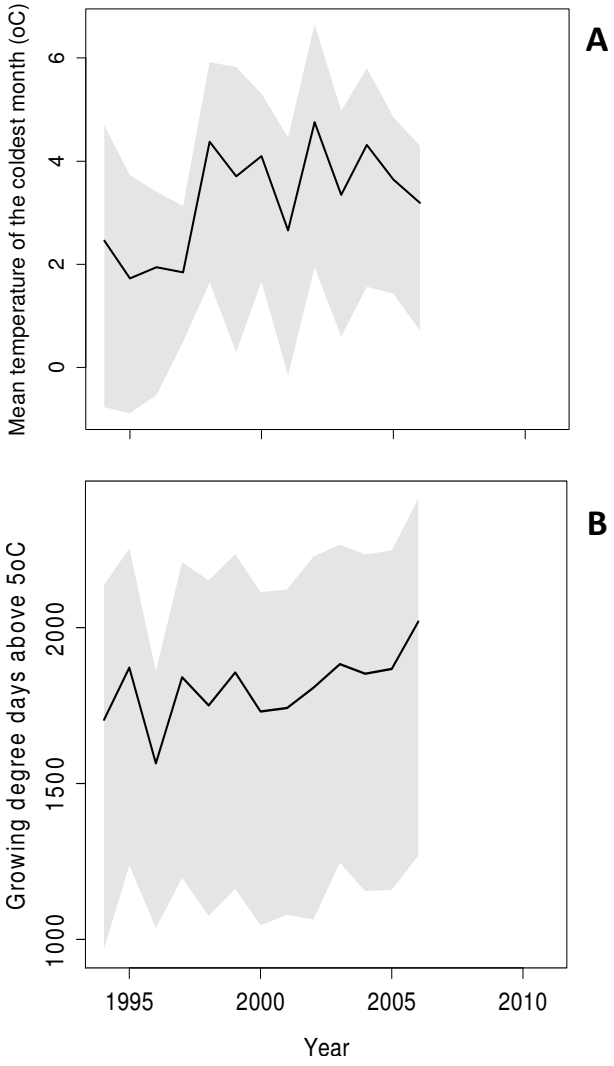


Figure S 2. Changes in mean temperature of the coldest month (MTCO; A) and growing degree days above 5°C (GDD5; B) over time, within the subset of 1811 Breeding Bird Survey sites included in the analyses (see Figure S 1). Grey polygons delineate the 95% confidence intervals around the mean values (solid lines) across the 1811 sites.

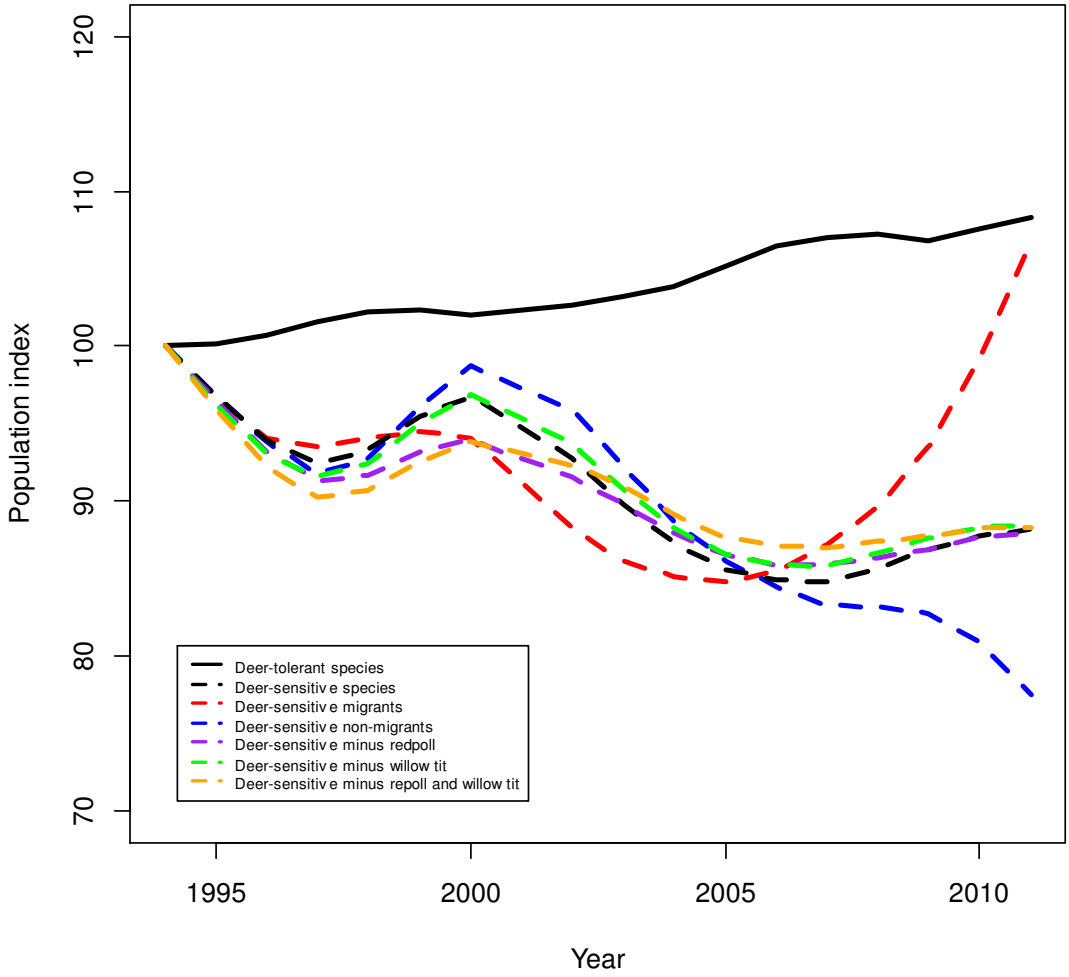


Figure S 3. Changes in the composite population trends of deer-tolerant (*n* = 16) and (different subsets) of deer-sensitive (*n* = 15) birds, in relation to population sizes in 1994. The lines show the geometric mean of the individual species population trends; anything above an index of 100 represents an increase in the index relative to the start year, and vice versa. Deer-sensitive species were split into migrants (*n* = 6) and non-migrants (*n* = 9) based on data from Robinson (2005) (see Table 6-1, page 126).